A Contribution

to the

Physiology of the Genus Cuscuta

BY

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Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 6.

Fig. 8.

Fig. 9.

Fig. 5.

Fig. 7.
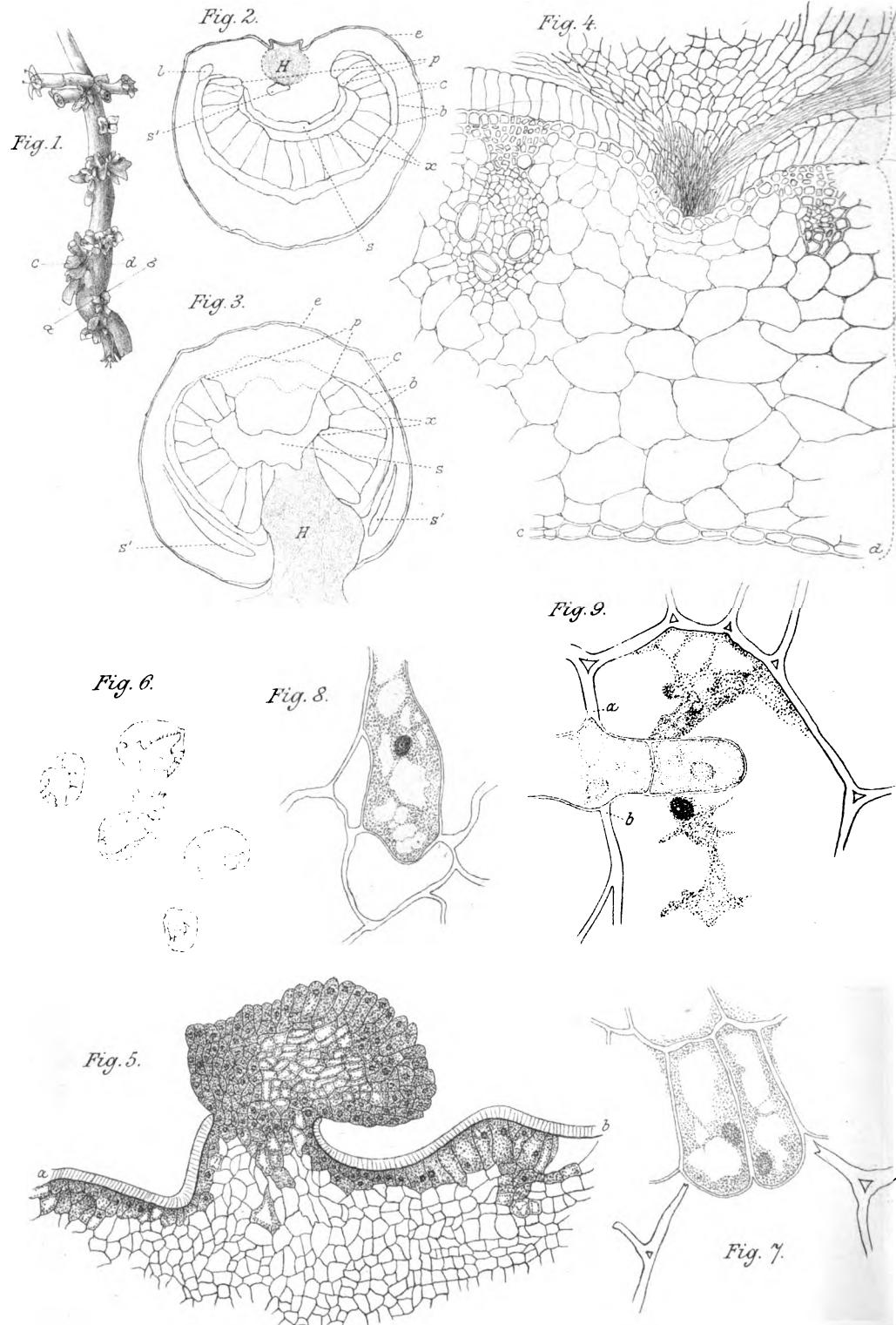
PEIRCE. — CUSCUTA.

A Contribution to the Physiology of the Genus Cuscuta [1].

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With Plate VIII.

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INTRODUCTION.

IN the course of an investigation into the origin, develop-
ment, and structure of the haustoria of certain parasitic
Phanerogams, the results of which were recently published [2],
a number of questions presented themselves which could not
be answered from alcohol-material, the only kind then avail-
able. Some of the questions concerned the members of the
genus *Cuscuta*, and required, for satisfactory study, consider-
able quantities of these plants alive and in all stages of
development. An abundance of such material was most
generously put at my disposal by Professor W. Pfeffer, of the
University of Leipzig, who very kindly gave me a place in his
laboratory and helped me at all stages in my work by sugges-
tions and criticism. The plants used were *Cuscuta Epilinum*,
Weihr., cultivated on *Linum usitatissimum*, L.; *C. europaea*, L.,
on *Urtica dioica*, L., and on various florists' varieties of *Chry-*

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[1] Diss. Inaug. at the University of Leipzig, 1894.
[2] Peirce, G. J., On the Structure of the Haustoria of some Phanerogamic Para-
sites, Annals of Botany, vol. VII, no. XXVII, 1893.

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santhemum; and *C. glomerata*, Choisy, on *Impatiens Sultani*, Hook., *I. Balsamina*, L., and *I. parviflora*, DC., &c. Of these the two larger, *C. europaea* and *C. glomerata*, proved most convenient for experimental purposes, owing to their own greater vitality, and also to the fact that their host-plants (except *Urtica*) bear confinement in a rather dry greenhouse very well. *C. glomerata*, an American species, is decidedly better for indoor study than *C. europaea*, attaining under such conditions a larger size than the latter, though differing from it in this respect only slightly out of doors; and the translucent character of its hosts, their large-celled pith and cortex (especially of *I. Balsamina*) make it an almost ideal plant for histological as well as physiological observation.

I began my experiments late in April, and continued them, without interruption, until the middle of August. Some of the material was raised from seed in the comparatively dry, at times cool, at times very hot, greenhouse which forms part of the botanical laboratory of the University of Leipzig. More of it was cultivated in the Botanic Garden: host and parasite were sown or planted together in pots in a frame, and when the hosts had become a few centimetres high, and the *Cuscuta*-seedlings had become well attached to them, the clumps of soil enclosing the roots were removed undisturbed from the pots and set into a warm, not too sunny, well-watered bed. Still more was sown with the seeds of the hosts, quite without precautions in dry and sunny, or in somewhat moist and shady, places. The rest of the material was taken by transfer (as will be described further on) from an unpotted to a potted host, and brought into the small greenhouse above referred to. Owing to the unusual dryness of the season, accompanied in May and June by longer or shorter periods of abnormal coolness, the plants out of doors were not so luxuriant, and did not so long vegetate, as in more favourable seasons, but came sooner and more compactly into bloom. As will be shown further on, these differences from the usual conditions have made clearer some interesting facts which otherwise might have escaped my notice.

From the time of Palm[1] and Von Mohl[2], who studied certain species of *Cuscuta* in the course of their investigations on climbing plants in general, these interesting parasites have been so much studied and written about that, for the sake of a tolerably complete presentation of the new observations which I have to communicate, I must repeat much that is generally known. The student of the plants of this genus is especially indebted to the papers of Ludwig Koch[3], and to the second of these I shall have frequent occasion to refer.

In this paper I shall consider *first* the formation of the haustoria, the conditions necessary for this and for their full development, the general relations of the parasite to its environment; and *second* the penetration of the haustoria into the host.

I. THE FORMATION OF HAUSTORIA.

1. *Germination and early growth.*

If the seeds of one of the three species of *Cuscuta* above mentioned be sown on moist earth, they gradually absorb sufficient water to double their size, and, in eight or ten days, germinate, pushing through the integuments of the seeds roots which are snowy white in colour. Such a root, short, thick, more or less spindle-shaped, devoid of a cap, and with short, though rather numerous hairs (their length varies directly with the amount of moisture), is very feebly geotropic and penetrates the subjacent soil for only one or two milli-metres, if at all. Instead of the cells of its central cylinder differentiating into vascular bundles, which are at first radial and separate, later, through secondary thickening, becoming collateral and confluent, the central cylinder consists of no lignified cells at all; the walls remain thin, and, though the

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[1] Palm, L. H., Ueber das Winden der Pflanzen, Stuttgart, 1827.

[2] Mohl, H. v., Ueber den Bau und das Winden der Ranken und Schlingpflanzen, Tübingen, 1827.

[3] Koch, L., Untersuchungen über die Entwickelung der Cuscuteen, Hanstein's Botanische Abhandlungen, Bd. II, Heft 3, 1874; Die Klee- und Flachsseide, Heidelberg, 1880.

cells become quite long, they retain throughout their brief
existence the appearance of young procambium-cells, being
filled with granular protoplasm enclosing large nuclei. This
core of thin-walled elongated cells, less like a vascular struc-
ture than the central cylinder of the larger Mosses (e. g. *Poly-
trichum*), is the only indication of the differentiated root-
structure which these plants must have possessed before
they became parasitic. The cortical cells are approximately
cubical, thin-walled, containing abundant protoplasm and
large nuclei. Indeed it is a noteworthy, as well as an easily
observed, fact that the nuclei of all the living cells of a *Cuscuta*
are larger than those of the corresponding cells of its host.
The epidermal cells and the root-hairs are slightly cutinized.

The root having penetrated the soil for a short distance, or
having grown sufficiently over the surface to give some sup-
port, the now rapidly elongating stem, having grown for some
distance out of the seed, bends at a point near its union with
the root and thus rears its tip, still enclosed within the seed-
coats and imbedded in the endosperm from which it draws its
nourishment, till it becomes nearly or quite erect. The young
stem is yellow or almost white, at any rate not green, and so
lacking in chlorophyll that assimilation must be very slight, if
at this stage of the plant's history it occurs at all. Frank[1]
cites in his text-book an investigation carried on in his labora-
tory by Temme[2], according to which chlorophyll is present,
not merely in quantity sufficient for spectroscopic determina-
tion, but also for the evolution of oxygen, as proved by
experiments with fuming phosphorus. Such investigations
were, however, carried on with older plants, and, though
necessarily implying the presence in the seedling of plastids
capable of developing into chloroplastids, scarcely yield
results which would justify our assuming that the seedling
obtains food from any other source than the endosperm in
which its tip is imbedded. (As to the amount of chlorophyll

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[1] Frank, A. B., Lehrbuch der Botanik, Leipzig, 1892, Bd. I, p. 556.

[2] Temme, F., Berichte der deutschen botanischen Gesellschaft, 1883, p. 485.
Also in Landwirthschaftliche Jahrbücher, 1884, Bd. XIII.

in older plants I shall have more to say further on.) The stem being now erect or nearly so, and continuing to grow in length, nutates in wider and wider circles or ellipses in search of some suitable object around which to twine. As first pointed out by Von Mohl [1], the seedling will not twine indiscriminately about any object whose size, form, and position one might suppose to be appropriate, if not directly to nourish, at least to hold it up in its efforts to reach a nutrient support, namely some living plant. Von Mohl tested this by pieces of wire and thin rods of fir-wood kept for three days in contact with the seedling. The plant refused to twine about them, though, when brought into contact with a plant of Nettle, it wound about it within nine hours. Koch [2] and others have confirmed this important observation, but without being able to account for the fact. Koch [3] says—'Der junge Schmarotzer besitzt somit in Bezug auf den von ihm zu befallenden Gegenstand eine gewisse Wahlfähigkeit, deren physiologischer Nutzen nicht zu verkennen ist.'

Through the integuments of the seed the embryo receives from the moist soil, or damp substratum of any sort on which the seed may rest, sufficient water to cause it to germinate, other conditions of temperature, &c., being favourable. The spindle-shaped and but feebly-developed root continues to secure moisture through its hairs from the substratum, and thus provides the necessary amount of water for the solution and transportation of the food-substances stored in the endosperm. The root is, however, a short-lived structure, beginning to die generally within seven days after its appearance, and hence it can supply only a small quantity of water in all. Under favourable conditions, primarily a damp substratum and a moist atmosphere, the root doubtless supplies enough water completely to convert the reserve food-materials in the endosperm into transportable and available solutions; but if, owing to the surrounding air being dry, the transpiration of

[1] Mohl, H. v., loc. cit.
[2] Koch, L., Hanstein's Botanische Abhandlungen, Bd. II, Heft 3, p. 110, 1874.
[3] Koch, L., Die Klee- und Flachsseide, Heidelberg, 1880, p. 17.

the seedling be greatly increased, and the neither thick-walled nor strongly-cutinized epidermal cells of the stem be unable to counterbalance the loss by their own absorption, the growth of the seedling will be greatly lessened in speed and amount, and thereby its chances of finding a suitable support will be diminished. Any dry object with which it comes into contact also draws water from it. Hence it is evident that, in this respect at least, it is disadvantageous to the plant to wind about dry and innutritious supports. The length to which the seedling can grow is proportional to the amount of water which it can absorb and retain, that is, to its turgescence. Seeds sown on sunny dry beds in the garden germinate slowly, the roots of the seedlings die soon, the stems attain a length of only a few centimetres, usually not more than five, unless a host be quickly found. If, on the contrary, the bed be a moist and shady one, or still better, if the seeds be sown on damp earth in a pot covered by a bell-glass, the seedlings can attain surprising lengths. Not only is the total amount of growth greater, but the length of the living part of the seedling is also greater. From the dying root most of the nutritive materials are removed to younger parts. Thus fed, the tip of the stem can continue to grow, and thus the area explored by it in its circumnutation is increased. Not only does the dying root yield its substance for the nutrition of the tip of the stem, but the stem dies also from below upwards, and from it too the nutritive substances are transferred to the youngest parts. Owing to the ability of the growing part to extract food from the oldest and least useful parts, the seedling is capable of a slow locomotion. The advantage of this is quite obvious, for in this way the seedling can approach a suitable plant which was at first beyond reach, and finally can lay hold on it.

If the root be not already dead before the seedling has found a host about which it can twine, it quickly dies when the youngest part of the stem begins to wind. The direction of winding in every case which has come under my observation was in the direction of circumnutation, namely the reverse

of the hands of a watch. The stem of the seedling, like the stem of the older plant, as I shall show later, is sensitive to contact-irritation for only a short distance from the tip and only in the growing part, and the irritability is greatest near the middle of the growing region, diminishing rapidly in both directions. If, therefore, the stem be brought by its nutation into contact with a host so that a non-irritable or only slightly irritable part be applied to the host, either no twining will take place, or only a loose steep spiral will be formed, until the irritable part touches. Then the *Cuscuta* rapidly forms one or more close spirals, the direction of the curved part of the stem being as nearly horizontal as possible. As I shall show later, the object of these close spirals is two-fold : they bring many more points of the stem into intimate contact with the host ; and they hold the stem, which would otherwise be pushed away from it by its own growth and by the growth of the haustoria, closely applied to the host. When such close spirals are made, haustorial formation is induced by the intimate contact. The origin, structure, and development of the haustoria were described and figured in detail in my previous paper[1]. Suffice it to say here that the haustoria originate, like typical roots, deep in the cortex, break through the overlying cortical and epidermal tissues, penetrate into the host and, attaching themselves to the vascular bundles, draw from them through tracheids and sieve-tubes the various solutions which they contain. Exactly how the haustoria make their way into the host was one of the questions which I set myself to answer, and of this I shall speak at length in the second part of this paper.

One or more turns in a short close spiral having been made about the host, the root, unless already dead, and the stem below the first point of contact, die quickly, yielding their substance as nourishment to the youngest parts of the seedling. The root and stem remain for only a short time as an empty, dry, shrivelled filament which the wind quickly snaps and blows away. The nourishment obtained from them

[1] Loc. cit.

enables the young plant to increase considerably in diameter where it has twined (an increase in size like that well known in tendrils[1]), to form haustoria, to develop the tabular epidermal cells overlying the nascent haustoria into long papillate cells, such as I have already described[2], and whose special functions I shall presently discuss. During the process of winding about the host, growth in length becomes slower, and finally almost, if not altogether, ceases, while the plant is increasing in diameter, forming haustoria, and sending them into the host. The haustoria having penetrated by the means which I shall describe later on, and having united their phloëm- and xylem-elements with the phloëm- and xylem-elements of the vascular bundles of the host, as I have described in the preceding paper[3], the young *Cuscuta* now receives an abundant supply of food. Much of this food it accumulates in solid form before it begins to grow again in length, as the abundance of starch-grains in the cortex indicates. When considerable quantities of reserve material have been thus accumulated, the plant, now entirely parasitic, grows for a time very rapidly, not only the main stem increasing in length but one or more buds, found generally two or three together in the axils of the small scales which are the only leaves that the plant has, rapidly develop into branches whose number, length, and thickness are proportional to the number of haustoria which the *Cuscuta* has been able to form, and upon the nutritiveness of the host.

The age and size of the host at the point where it is attacked greatly influence the parasite. If the host be of considerable diameter, two centimetres for example, the seedling will usually fail to effect a single turn about it : or if it be one-and-a-half centimetres, the parasite can make only one turn, and thus will not clasp firmly enough to enable many haustoria to penetrate ; hence the supply of food obtained will not be

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[1] Darwin, C., Movements and Habits of Climbing Plants.
[2] Peirce, G. J., loc. cit.
[3] Id., loc. cit., p. 295.

favourably proportioned to the effort made to secure it, and the *Cuscuta* often succumbs under such conditions. If, however, the host be one centimetre or less in diameter, the seedling, unless exhausted by the length to which it has already been obliged to grow in order to reach a host, can make a number of turns, will clasp the host tightly, will form many haustoria in consequence of the extensive area of intimate contact, and will therefore be the more likely to obtain abundant nourishment. The maximum diameter of a stem or branch of a living plant around which a seedling can twine varies with the species of *Cuscuta,* the larger species, and naturally also the larger seedlings of the same species, being able effectually to embrace larger hosts than the smaller ones. One and a half centimetre is the mean maximum for *C. Epilinum,* and two centimetres for *C. europaea* and *C. glomerata.* I am unable to give the minimum. I have seen, however, seedlings winding successfully about stems of one millimetre in diameter. Since older plants, even of the larger and therefore, for mechanical reasons, less conformable species, find no difficulty in winding tightly about, and even forming incipient haustoria against, silk and cotton threads of a mean diameter of one-third of a millimetre, there is little reason for supposing that, other conditions being favourable, a seedling could not wind closely about and send haustoria into a host of no larger diameter.

The part of the host attacked need not be cylindrical in form, as the frequent observation of seedlings, as well as older plants, which have applied themselves to the lamina of various sorts of leaves, proves. In such a case the very sharp turn which the stem of the parasite is able to make allows it to apply itself to both the upper and the under surface of the leaf. The whole curve thus made is an ellipse, one of whose diameters may be very short, the other proportionally very long. Such an ellipse made by a seedling around a leaf had a long diameter of one centimetre and a half, a short diameter of two millimetres. A similar curve made by an older branch of *C. glomerata* had as respective diameters a line nearly

three centimetres long and another one millimetre long. By the great range of curves which these parasites can make, they are enabled to conform themselves to the most variously-shaped parts of their hosts.

Another quality of the host must now be considered, however. If the first plant about which a seedling of *C. glomerata* lays its coils be an *Impatiens* of one of the three species mentioned above, the haustoria will penetrate easily and find abundant nourishment. But if the seedling fastens itself upon some other plant its chances may not be so good. If the plant be a hard and comparatively innutritious Grass, or a tolerably woody herb or shrub, the haustoria will penetrate more slowly and will secure less nourishment, and hence the parasite will not so soon be able to develop its stem and branches, or so abundantly. Thus its chances of quickly finding a more nutritious host are lessened. The success of the *Cuscuta*, its dangerousness as a parasite, depend in the first place upon the number of seeds each plant forms, upon the distribution of these in places where many herbaceous plants grow close together, where the ground is moist, or where the abundance of larger herbs form a covering under which a moist atmosphere is confined, and hence where transpiration is not excessive.

2. *Conditions necessary for the formation and development of haustoria.*

The quickly-growing main stem and branches enable the young parasite to reach out in many directions, to lay hold upon the branches of its host, upon other plants, and indeed upon all objects which can mechanically support it, be they wet or dry, smooth or rough, living or dead. When the plant has secured a suitable host and has entered upon the period of healthy activity which an abundant supply of food ensures, it is in the most suitable condition for experiment.

After a period of short close winding about a host, a period

of but slow growth in length, of considerable increase in thickness, of active development of haustoria, there follows a period of long loose winding, of rapid growth in length, of slight increase in thickness, and of no development of haustoria. The biological advantage of this alternation in mode of growth is great and evident. During the period of rapid growth in length the parasite greatly increases the area, often also the number of plants, from which it may draw food. During the period of slow growth in length it fixes itself at many points in this area and develops the haustoria which are to supply it with food. The means by which these alternations in mode of growth are accomplished must now be considered.

As stated above, though the seedling will not twine about dry and dead organic supports, or rods of glass and metal, yet the young plant, feeding itself from the host upon which it has fastened, will do so. Hence, in the following experiments, rods of wood, glass, glass covered with filter-paper, wires, strings, and threads, as well as plants, can be used, provided none be too large in diameter. It makes also no difference, as will be shown presently, whether the rods be wetted throughout the course of the experiments or remain dry.

If now one of the objects named be brought into contact with one of the young and rapidly developing lateral branches, or with the main stem when it begins rapidly to grow after forming haustoria, though the contact be carefully maintained, either by frequently moving the rod in correspondence with the change in direction or the increase in length of branch or stem, or by fastening the branch or stem to the rod in any way (best by a narrow ribbon of gummed paper), the *Cuscuta* will make no close turns about the support. If it follows the support, as the more or less erect main stem is likely to do, and as the more nearly horizontal branches are not likely to do, only a long, steep, loose spiral will be formed. After a time, however, the growth decreases in rapidity. If now a contact be made about three centimetres from the tip, the stem or branch will bend sharply and, in the course of fifteen

hours, make two or three short turns closely around the
vertical rod.   Within the next fifteen hours more such turns
may be made, and it will be evident from the swellings on the
side of the *Cuscuta* next to the support, that haustoria have
begun to form.   If the contact between the *Cuscuta* and the
vertical rod be made at a point only about one centimetre
from the tip of such a more slowly growing part, there will
be little or no effect.   If the point of contact be too far from
the tip, more than six or seven centimetres for *C. glomerata*,
there will also be little or no effect; if far enough back,
absolutely no effect.

The parallel of such a condition of affairs is exactly
furnished by tendrils, for example of *Passiflora gracilis*, Link.
A wooden, metallic, or glass rod placed in contact with
a young, short, and rapidly-growing tendril, whether the
point of contact be near the tip or the base, or in the middle,
will produce no effect.   When, however, the tendril ceases to
grow so rapidly, having attained a length of several centi-
metres, on such a rod being brought into contact with it at
a point about three centimetres from the tip and against the
side toward the direction of nutation (the concave side),
twining will take place.   If the contact be made at or very
near the tip, or in the region nearer the base which has ceased
altogether to grow, there will be no effect.   Every one knows
that the tendrils are sensitive to irritation by contact, and it
is the general opinion that the stem of *Cuscuta* is so also, but
so far as I am aware no sufficient proof of this has yet been
adduced, though since Von Mohl first made the statement in
1827 many have studied the plants of this genus in various
ways.   In a very suggestive paper by Pfeffer[1], one finds an
account of a series of interesting experiments on tendrils, in
which it is clearly shown that fluids (unless they are poisonous
or contain solid particles in suspension) produce no irritation
by contact.   Pfeffer found also that gelatine, if kept wet, also
produced no irritation by contact, but, when allowed to dry,

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[1] Pfeffer, W., Zur Kenntniss der Kontaktreize, Untersuch. aus dem Bot. Institut
zu Tübingen, Bd. I, p. 483 et seq., 1885.

at once induced the usual turning of the tendrils. At Professor Pfeffer's suggestion I undertook to test the irritability of *Cuscuta* by means of gelatine. If the *Cuscuta* wound about a rod coated with wet gelatine, forming short close turns, there must be some reason other than contact-irritation (perhaps a chemical one) for their formation, for *Cuscuta* does not of itself and unstimulated make such close spirals ; though old tendrils which have not succeeded in finding a support normally do. If, on the other hand, the *Cuscuta* made only long, steep turns, if any, we should have positive evidence in support of the idea of contact-irritation.

According to the paper just cited, it makes no difference in its effect on tendrils whether the gelatine be simply soaked in water till it will absorb no more, or whether it be dissolved in proportions of eight per cent. or less in water. For reasons of mechanical convenience I preferred to use concentrated gelatine. I coated, as smoothly as possible, a glass rod of two or three millimetres diameter and twenty centimetres length, for a distance of fifteen centimetres, with gelatine to which only enough water had been added to make it rather soft when heated over a water-bath. In order to allow for its absorbing more water and swelling later, the coat of gelatine was made not more than two millimetres thick at this stage. Around one end, the end of the rod not coated, I wound several layers of filter-paper, enclosed this in stiffer paper, and tied it fast together, thus making a cup, out of the bottom of which, when the rod was held vertical, water could flow in a thin sheet over the whole rod of gelatine. Into a chamber made of a bell-jar held mouth upwards on a retort-stand (as shown in the annexed woodcut), covered by a glass plate pierced in the centre by a hole one and a half centimetre in diameter, and kept moist by a thick band of wet filter-paper (*a*) laid inside, I introduced a branch of *Cuscuta Epilinum* (*c*). Through the hole in the glass plate above I passed the gelatine-coated glass rod (*g*), fastening it at the top and resting its lower end in the mouth of a tube (*d*) which ran to a catch-bottle (*b*) below. From a reservoir (*w*) above

a constant supply of water was conducted by a fine siphon (*s*) into the paper cup (*e*) at the upper and uncoated end of the gelatined rod. From this cup the water flowed slowly and uniformly over all parts of the gelatine and was conducted away by the drainage-tube (*d*) to the catch-bottle (*b*). The hole at the bottom of the moist-chamber was closed by cotton wadding and the hole in the glass cover was nearly closed by a split cork. In the course of its circumnutation the *Cuscuta* came into contact with the rod, the nutation was delayed by the rigid obstacle, but the stem did not twine. Later, however, contact with the gelatined rod having been repeatedly broken and renewed in the course of the nutation of the stem, the plant began to climb up the rod, making long, steep turns about it. These processes lasted eight days. On the ninth day, the stem, having reached the upper and uncoated part of the rod, at once made short, close turns about the glass and began to form haustoria. Control experiments with uncoated rods of glass and wood, wetted and dry, of rods coated with gelatine but not wet, in similar moist chambers, showed that contact always induced the formation of close turns and of haustoria. Hence it is evident that it was not the water which inhibited close winding, but merely the non-irritant nature of wet gelatine.

These experiments repeated with plants of all three species invariably gave the same results. We see, therefore, that the formation of close turns is always dependent upon contact-irritation ; that *Cuscuta* is, as others have asserted, irritable to
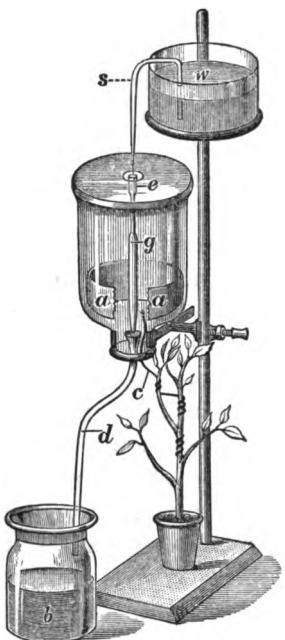
contact. Previous authors have pointed out, but without proving the fundamental fact of its irritability, that *Cuscuta* in its two modes of twining alternately resembles twining-stems and tendrils. It is generally admitted now, despite the efforts of Kohl [1] to prove the contrary, that climbing-plants climb by the combined action of nutation and geotropism, and that most climbing-plants are not irritable to contact. (*Lophospermum scandens* is one of the exceptions, its stems being slightly and its petioles considerably irritable.) When irritation is not produced, either through the absence of all contact with irritable parts, or through the contact of a non-irritant such as wet gelatine, the plant grows and climbs only as other climbers do, making long, steep turns about the support. Like tendrils, the stem is not sensitive in regions of no growth in length, or in regions and at times of most rapid growth, but is sensitive at times and in regions of moderate growth.

It is known that in the case of tendrils the effect of contact is not immediate, nor is it necessary that the contact should be permanent to produce winding. If momentary contact be made with very sensitive tendrils, for example those of *Passiflora gracilis*, Link, and *Sicyos angulatus*, L., decided bending toward the side on which the contact was made takes place. More slowly, if the contact be not renewed, the tendril returns to its former position. The process of twining is therefore *induced*, a short period of contact inducing a comparatively slight and temporary bend, a longer one having stronger and more permanent effects, till finally a point is reached when withdrawal of the irritant object causes no return to the primary position of the organ, the induction having produced permanent effects. With tendrils less sensitive than those just mentioned, such striking effects are not produced, yet the principle remains the same. Now experiment shows that when the contact of an irritant object with the irritable part of the stem of a *Cuscuta* produces certain effects, these effects are not immediate but are *induced*; that

[1] Kohl, F. G., Beitrag zur Kenntniss des Windens der Pflanzen. Pringsheim's Jahrbücher für wissenschaftliche Botanik, Bd. XV, 1884, p. 327, &c.

if the contact be not long continued the effects, though plainly evident, are only temporary ; and that contact with an irritant object need not be permanent to produce permanent effects. But *Cuscuta* is by no means so sensitive as the most sensitive tendrils. Negative geotropism plays a much more important rôle than in the case of tendrils ; for repeated experiments show that the parasite will not twine about horizontal branches or rods, even though they be rough and thereby strongly irritant. If one complete turn be made about a vertical rod and the plant be evidently ready to make more, it will not continue to do so if the support be laid horizontally ; but on the other hand it will only partly, if at all, undo the turn which it has already made. Also, if two or more close turns be made around a vertical rod, the formation of haustoria will not be prevented or delayed by placing the rod horizontally.

It is now evident that the short close turns of the *Cuscuta* about its host, or about any other support of suitable diameter, are induced by contact-irritation. It is also plain, from the observations of many authors, that haustoria are normally formed in nature only on such close turns. But is it necessary for the health of a branch that it form such close turns ? And are such close turns necessary for the formation of haustoria ? Both questions can be answered in the negative, as the two following experiments show.

A strong horizontal branch of *C. glomerata*, springing from the axil of a bract borne on a stem just above a region where many strong haustoria had penetrated a very nutritious branch of *Impatiens Sultani*, was allowed to grow horizontally without contact with anything, until it had reached a length of fifteen centimetres or more ; then it was supported at a point far enough behind the tip to be no longer irritable. It continued to grow horizontally, and supports were applied at suitable distances. Finally at the end of three weeks, having sent out numerous branches (which I cut off lest, in the crowded greenhouse, they should by accident come into contact with some other plant, and so vitiate the results of the experiment), the main branch, large, healthy, in normal con-

dition so far as I could see, for its whole length, and still growing, had attained the surprising length of one metre! . This experiment shows not only that close turns are unnecessary to the healthy nourishment and perfect development of a branch, but also that the nourishment secured by the haustoria of one part can be transported over great distances to those parts which are not fed by haustoria of their own. In this latter respect it makes little or no difference whether a horizontal or an erect branch be used ; for a branch allowed to twine on a long vertical glass rod, from which it can of course draw no nourishment though it may make close turns about it and begin the formation of haustoria (which soon abort, however), will attain a very considerable length at the same time that its healthy appearance is preserved.

To show whether or not close turns are necessary to the formation of haustoria, the following experiment was undertaken. A branch of *C. glomerata*, in suitable condition to wind closely and to form haustoria if conditions favoured, was enclosed between the upper faces of two leaflets of a *Phaseolus* still attached to the petiole, whose lower end dipped into a bottle of water. The leaflets were kept so closely applied against the *Cuscuta* between two plates of glass of convenient size (e. g. 8 cm. long and 4 cm. broad) that it could make no curves except in the plane parallel with the surface of the leaves and glass. The glass plates were held firmly together by a stout paper band around each end. In order to prevent their crushing the leaflets and the *Cuscuta* which were pressed between them, a strip of glass, two millimetres thick, was placed between them at each end. In this way a constant contact, accompanied by considerable but not dangerous pressure, was maintained for three days. That the branch was perfectly healthy was shown by its continuing to grow in quite normal fashion. At the end of three days the apparatus was taken apart, and it was found that the parasite had made no curves, even in the plane parallel with the glass plates, but that it had formed haustoria which had entered the leaf-tissue. It is, therefore, plain that close windings are not of them-

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selves necessary to the formation of haustoria. They are simply a means, and the easiest and most effective one, of bringing a considerable area of the stem or branch of the *Cuscuta* into intimate contact with the host, and of maintaining this contact. If intimate contact be formed and maintained over a considerable area in any other way, which is rarely the case in nature, the haustoria will be formed without the usual preliminary of winding.

It has been asserted by L. Koch[1] that the stems and branches of these parasites can, and sometimes do, twine closely about a host in the opposite direction to their nutation, and then form haustoria as usual on the side in contact with the host. I have not had the good fortune to see such plants. Experiments show, however, that *Cuscuta* is not more irritable on one side than on another. In the experiment just described, where a branch was enclosed between two leaflets, the contact and pressure were alike on both sides. Haustoria were formed on both sides penetrating the two leaflets equally well, the haustoria generally alternating in sets of three on the two sides; but some haustoria were directly opposite one another.

If a young branch growing quite free be marked with a straight longitudinal series of dots for a distance of five centimetres from the tip, it will presently become evident that, both in free growth and in the formation of close turns after contact with a host, a decided torsion of the stem takes place, and that the line of haustorial development does not bear any definite relation to this line of dots. From the absence of bilaterality in the stem, there is no reason why, when the close turns have once been made in the direction opposite to the nutation, the haustoria should not develop. To overcome the tendency to nutate in one direction, and to bend sharply and for a time continuously in the opposite direction, might require very strong irritation; or it might be that some plants of this genus (as in a few others[2]) nutate

[1] Loc. cit., 1880, p. 18.
[2] Compare Darwin's Climbing Plants, about *Scyphanthus elegans*, &c.

alternately in one, then in the other direction, twining accord-
ing to the varying direction of nutation. Such alternation
I have not seen. There is the further possibility that in some
the tendency to nutate in a given direction is weaker than in
most plants, and that therefore the irritation need not be
unusually strong to cause winding in the opposite direction.
Koch says it is not common for such turnings to be made.
A very large majority undoubtedly twine in the direction of
nutation, in the reverse direction to the hands of a watch.
There is no more reason, however, why some plants should
not twine in the opposite direction constantly, or in both
directions alternately, than that there should not be left-
handed or ambidextrous men and women.

I have said above that the object of the close turns is to
produce and to maintain an intimate contact between the
parasite and its host for the purpose of developing haustoria.
I have shown too that the process of twining closely is one
which is *induced* by contact, following it after a longer or
shorter interval. It may now be asked if the formation of
haustoria is also induced by contact-irritation, and will be
continued even after the contact has ceased to exist? To
answer this question a number of experiments were under-
taken.

If a branch of *Cuscuta* be brought into contact with a host
and, after having made two or two and a half close turns
about it and being about to form more, be gently removed
from it and held from below in the same general direction, the
branch will, like a tendril, continue to twine for a while.
During the time necessary for the formation of two turns
about the host, the contact will have been so protracted as to
ensure the permanence of at least the lower one of these
turns, but the time is too short (being about ten hours for
C. glomerata) for any external evidence of haustorial formation
to become visible. In the course of the next twenty-four
hours, the usual swellings on the concave side of the curved
branch will become evident, and these will continue for some
time to increase in size. They are produced by the formation

of haustoria deep in the cortex, which push out the overlying cortical and epidermal cells. No change in the form of the epidermal cells takes place, though they must multiply in order to maintain an unbroken covering for the stem. After the swellings have ceased to grow, sections of them show that the haustoria attained a greater or less development in proportion as the part of the stem was in longer or briefer contact with the host; but in no case where the contact was not permanent was there a complete development.

That haustoria never begin to form without contact has been repeatedly shown by placing branches which are ready to form haustoria, whenever the conditions become favourable, in various nutrient solutions. Haustoria never form in such circumstances. If, however, a rod of suitable size be brought into contact with the submerged branch, feeble twining will take place and sometimes haustoria will be begun; but the process of twining and, as a consequence, the formation of haustoria are hindered by the fluid. The hindrance is doubtless mainly of one sort, that which reduces the irritating effect of the rod. This result resembles in kind, though not in degree, those obtained by similar experiments with sensitive tendrils[1]; but owing to their greater sensitiveness to the contact of solid bodies, the fluid, be it water or anything else not poisonous, does not so greatly reduce the amount of twining. Evidently contact is absolutely necessary for the beginning of haustoria, and it is plain too that the formation of haustoria is an induced process, just as the winding of tendrils and the formation of short, close turns are induced processes.

The swellings just mentioned as being produced by the outward pressure of the growing, but soon aborting, haustoria, differ in shape from those formed when the parasite remains at those points in contact with a host-plant. These swellings, the results of the arrested growth of haustoria, are conical in form and are covered by flat and somewhat elongated

[1] Pfeffer, W., Zur Kenntniss der Kontaktreize, Untersuch. aus dem Bot. Institut zu Tübingen, Bd. I, p. 483 et seq.

epidermal cells exactly like those on other parts. The swelling produced by the growth of a constantly-developing haustorium under a point of continued contact with a host, is broader and not so high, and is surrounded at a little distance by a ring-like elevation of about half its height. Longitudinal sections show, as I have already described and figured[1], that the central elevation is formed by the pressure of the subjacent growing haustorium, and is covered by thin-walled, papillate epidermal cells of very considerable length and abundant protoplasmic contents; that surrounding this are a few rows of shorter, but still papillate, epidermal cells of similar character; that beyond these are several rows of long, papillate epidermal cells, these alone forming the elevated ring surrounding the central protuberance; and that beyond this the epidermal cells remain typical in form and contents. We see plainly that not only is the formation of close spirals and of haustoria a result of contact-irritation, but that the changes in the epidermal cells are also due to this cause. As will presently be shown, however, the complete development of the haustoria and a complete modification of the overlying and immediately adjacent epidermal cells is not the result of contact only.

Ludwig Koch[2] has clearly described that, when the parasite has made one or two close turns about a branch of its host and does not continue winding about this, but makes at once a similar spiral about the petiole of a leaf, which springs at that point from the stem of the host, that part of the *Cuscuta* between the last point of contact with the stem and the first point of contact with the leaf will, like the adjacent regions, bear haustoria. But the haustoria in this intermediate region will not develop far, and we shall see instead the conical swellings which Koch denotes 'sterile Haustorien.' He ascribes their formation, like that of normal active haustoria, to irritation; but he fails to make clear whether he believes them to be the result of irritation by contact at the points where they appear, or whether they are induced to form by the contact

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[1] Loc. cit., p. 295. [2] Loc. cit., 1880, p. 50.

of the stem with the host on either side. To put the question directly—Is each haustorium induced by contact immediately over its point of origin, or can haustoria be induced to form between two points by contact at these two points only? The question may readily be answered by marking the growing and twining stem with Indian ink at the last points of contact with the host, and bringing against it, at a distance of one centimetre or less, either another host or a rod of suitable size. When the *Cuscuta* has made one or two close turns about the support, it will be noticed that the dots which were over the last points of contact with the host have now been brought by growth into the region intervening between the host and the new support, and that when haustoria appear there they form at or behind those points, not in front of them and towards the tip, and somewhat earlier than those on the part of the parasite which is in contact with the new support. If they were induced between the points of contact, no contact having ever existed in the region of their origin, they should appear at the same time as or later than those against the support. Their earlier appearance and the change of position of the dots make it quite evident that they are the results of contact at the points where they originate and that their abortion is due to the contact being only temporary. Each haustorium is, therefore, the result of irritation produced by contact at the place where it forms.

I said above that contact alone, though sufficient to induce the formation of haustoria and to cause some changes in the overlying epidermal cells if continued long enough, is not sufficient to secure the full development of haustoria or to produce extended changes in the epidermal cells. It has often been observed that when a branch of a *Cuscuta* has wound itself in a close spiral about a rod of glass or wood that, though the haustoria are formed, as shown by the swellings on the concave side of the stem, and also by sections, they do not develop very far. Sections show further that, though the epidermal cells at the points of contact and over-lying the nascent haustoria do elongate slightly, no such

marked difference between them and those adjacent is to be
seen, as has just been briefly described as existing when the
parasite is in similar contact with a host.   That it is not the
dryness of such rods of wood, glass, paper, or whatever the
material may be, which stops the development may easily be
shown.   If water be made to flow gently and constantly over
such rods, the epidermal cells differentiate little if any more,
and the haustoria do not develop any more, than if the rods
remain dry.   If, after haustorial formation has been strongly
induced by a wet or dry rod, the rod be withdrawn and the
branch be enclosed in a moist chamber made of a piece of
large glass tubing, sand being carefully poured into the tube
and around the branch to a height just above the last turn,
and wetted with distilled water, both ends of the tube being
closed by corks, no more development of haustoria takes
place than has already been described as occurring when the
contact is only temporary.   This experiment shows plainly
that it is not the hardness of the rods which causes the epi-
dermal cells to remain only slightly differentiated and the
haustoria abortive, for the haustoria could easily penetrate
between the comparatively loose particles of sand, and surely
the sand would cause sufficient irritation, if contact were all
that is necessary to cause a full development of these two
structures.   The sand used was first treated with strong
hydrochloric acid to remove all calcium salts, washed on
a filter with distilled water till the filtrate gave no acid
reaction, then heated for a quarter of an hour over a Bunsen
flame to carbonize all organic matters not decomposed by the
acid, and finally cooled and poured into the glass tube, which
had previously been washed with strong alcohol and then
with distilled water.   Of course the cork which is used to
close the lower end of the glass tube must be cut in halves,
and a groove, large enough to enclose the branch of *Cuscuta*
without pressing it closely, be made between the two pieces.

Thus we see that the continued contact of an easily pene-
trable substance is not sufficient to induce full development
of the haustoria and of the overlying epidermal cells; nor are

moisture and contact combined sufficient.   One naturally inquires if the nourishing character of the host has anything to do with the rapid and full development of these structures. To answer this question is easy.   If, after having induced haustoria by contact with a rod of some sort, taking care that the contact be only long enough to induce the formation of haustoria and not long enough for the innutritiousness of the rod to have any repressive effect on them, one inserts the branch into a glass tube as above described, closing the tube at the bottom with a split and grooved cork, but sealing the hole by a few drops of cocoa-butter or a little gardener's wax, and pours into it a decoction of the usual host-plant, one sees that the haustoria develop little more, and that the epidermal cells are only slightly longer than when they are pressing against a rod of glass or wood.   Hence it is plain that contact lasting until the formation of haustoria has been induced, and followed by a supply of nourishment in solution, are not sufficient to produce the effects which are evident when contact with a host is uninterrupted.

It must be admitted, however, that there are two quite unnatural elements in this experiment, namely: first, the superabundance of food immediately available if the plant can absorb it, and second, that this food is equally abundant on all sides.   To eliminate both of these errors I induced haustoria to form on a healthy branch of *C. europaea* by contact with a wooden rod, and then substituted for the rod a stick of elder-pith, of about the same size, which had been soaked for some time in a hot decoction of *Impatiens Balsamina* which, as sections showed, had penetrated for at least a millimetre from the surface.   I enclosed the branch thus wound around the elder-pith in a glass tube as before, keeping the air inside moist by means of wet filter-paper, and closing both ends by corks.   In the course of nine days the *Cuscuta* had continued to wind closely, making in all five complete turns about the pith.   Along the inner surface of these turns were as many haustoria as would normally be formed in an equal distance, and gentle pulling showed that

the parasite was by some means closely fastened to the pith. Cross-sections through the haustoria and the pith showed several interesting features. The epidermal cells were quite as long, papillate, and thin-walled as if they had developed in contact with a host-plant; their protoplasmic contents were only slightly less abundant and granular than in normal conditions; and they had penetrated the second, in some cases the third, layer of parenchyma-cells. (Of the mode of penetration I shall have occasion to speak in Part II of this paper.) The haustoria underlying these well-developed epidermal cells had advanced very considerably in their development, and were evidently pushing themselves against and through the adjacent cortical cells, though more slowly than normal. Their structure was as complete as that of young haustoria about to penetrate a host but still imbedded in their cortical matrix. That they were not farther developed, had not penetrated the overlying cortex and entered the stick of pith is not surprising; for the pith, though impregnated to a distance of a millimetre or more from the surface with a decoction of a plant, was nevertheless a comparatively innutritious substance. The decoction at first contained somewhat more nutritive matter than would at once be available in a host, but it was not constantly renewed as is the case in the living host, and it was likely to be very largely consumed by the epidermal cells, and also by the Bacteria and Fungi which are so difficult to exclude when it is not possible completely to sterilize everything used in an experiment. Yet the almost complete development of the epidermal cells, and the very considerable development of the haustoria plainly show, when taken in connexion with the results of the other experiments just described, that neither contact alone, nor nourishment alone after a period of contact, is sufficient for the complete development of these two associated structures. Both continued contact and abundant nutrition from without are necessary for full development.

I have previously pointed out that food taken into the parasite in one region can be transferred to another region at

a considerable distance which, because it lacks haustoria, is receiving no nourishment from outside. The distance to which food can be transported is dependent, of course, upon the nutritiveness of the host and the health of the parasite. One might suppose that, were the parasite strong and well fed, it would supply to a region in which haustoria had begun to form, all the nourishment necessary for their complete development, and also for the development of the overlying epidermal cells. Such does not seem to be the case, as the preceding experiments show. There is a manifest biological advantage in this; for any support which cannot furnish nourishment sufficient for the development of these two structures would also be innutritious even when the haustoria had penetrated it. The parasite tests the nutritiveness of the support by the cells most closely in contact with it. If these develop, the nourishment which they receive and pass on stimulates the associated structures to develop also. If they do not develop because of the lack of nourishment from without, there is no stimulus and no growth of the associated structures ; plainly an economy of material and of energy.

How comparatively unimportant to the part forming haustoria the food which it receives from other parts of its own body is, can be plainly demonstrated in the following way. Koch[1] pointed out that pieces of the younger parts of the parasite, if cut off, behave like the seedlings ; they nutate, they make close turns about a host when they come into contact with one, they form haustoria. He does not say that such 'cuttings,' if one may apply a gardener's term to them, resemble the seedlings in that they too refuse to twine about other than nutritious supports, and thus differ from their condition when still attached to the parent plant. This is, however, not the case ; here the resemblance ends. These cuttings, just as if they were still attached to and receiving nourishment from the parent plant, will twine closely about sticks of wood as well as about a host, and will also begin the formation of haustoria.

[1] Loc. cit., 1880.

If one cuts off branches of *C. glomerata,* for example, about six centimetres behind the tip, that is, cuts off the growing region, which naturally would not be likely to contain a large surplus of food, and fastens these cuttings by little ribbons of gummed paper upon the stems and erect branches of a suitable *Impatiens,* they soon begin to make close turns, and to develop haustoria which penetrate the host in the same length of time that they would consume were they still attached to the parent plant. To accomplish this large amount of growth they must have received food from outside, namely from the host about which they have twined. This food can at first have been absorbed only by the papillate epidermal cells, for these alone were in contact with the host. As has been shown before, these epidermal cells not merely come into and remain in contact with the epidermal cells of the host, but they penetrate these and therefore can absorb from the subjacent cortical cells which are richer in nutrient substances. Until the haustoria have themselves entered the host, these epidermal cells absorb all the food which the parasite receives from without. They are therefore, in a physiological sense, *pre-haustoria,* though in a morphological sense they are quite distinct from haustoria.

Although these cuttings have made close coils, have formed haustoria, have sent these into the host, as quickly as if they had remained attached to the parent plant, yet certain differences are plainly to be seen between them and others which have performed the same operations while remaining unsevered from the parent. In both the cuttings and in the still attached tips, growth in length nearly, if not entirely, ceases when the formation of close coils begins; but in the attached tips a marked increase in thickness follows the close winding, while no such evident growth in diameter takes place in cuttings, though a slight increase in thickness is sometimes observable. Owing to this growth in thickness of the attached tips and the consequent increase in the rigidity of the coils, the haustoria, in entering the host, are unable to push the parasite away, but all the pressure which they exert by their

growth is expended in penetrating the host. The haustoria formed by the cuttings, on the other hand, not having in the comparatively slender curved stems a rigid base against which to press and thus to make all the force produced by their growth tell in the penetration of the host, push the parasite away from the host, thus wasting force and increasing the distance through which they must grow in order to reach the conducting tissues of the foster-plant.

Still another difference between these two is also evident, namely, in their colour. The colour of the unsevered branches resembles that of the rest of the plant, varying from a straw-yellow to a decided orange, according to the nourishment and illumination which they receive. Ill-nourished and therefore thin plants are pale, no matter how well illuminated ; but the better the illumination which well-nourished plants receive, the more intense becomes the colour. The colouring-matter is situated in small chromoplastids, orange in hue, which the cells of the central cylinder contain in much larger numbers than those of the peripheral layers. With the ordinary microscope no chlorophyll-granules can be distinguished, though the presence of chlorophyll, as previously stated, has been shown by Temme by micro-spectroscopic methods. In and about the flower-clusters of all the species of *Cuscuta* which have come under my observation there is always an amount of chlorophyll sufficient to be recognized by the microscope, and often these parts are decidedly green.

Turning now to the cuttings, one sees that, though they may have been deep orange in colour when cut, the colour has begun to change before twenty-four hours have expired, and within forty-eight hours they have become distinctly green. *C. europaea* changes more slowly than the other two species, yet this plant too becomes green within two days after cutting. Longitudinal sections show plainly that many chlorophyll-granules of very considerable size have been developed, and that their distribution is the reverse of that of the chromoplastids above mentioned, since they are much more abundant in the cortical parenchyma than in the central cylinder. Their

localization in the more superficial and hence better illuminated cell-layers, rather than in the central and comparatively dark tissues, confirms the opinion that they are functional. I have not attempted any chemical experiments to determine the amount of oxygen evolved. It is to be noticed further that if, instead of cutting off only about six centimetres of the tip of each branch, the cutting be ten or more centimetres long, there is less development of chlorophyll and more growth in thickness of those parts which have coiled closely around the host; and that, as the root and the lower parts of the stem of the seedling yielded the nutrient matters which they contained to the younger upper parts and died, so the lower parts of the cuttings decrease in size, shrivel, and die. Evidently their substance is taken away and consumed by the younger coiling parts. But as the preceding experiments show, no matter how much nourishment the part which is forming haustoria can secure from the other parts of the parasite, this is sufficient only for the growth in thickness which normally accompanies the formation of close turns around the host, and to forestall the necessity of developing chlorophyll-granules; it is not sufficient for the full development of the epidermal prehaustoria and of the haustoria proper.

The development of chlorophyll in these parasites is always a consequence of insufficient food, as the following experiments indicate. I raised three sets of *C. Epilinum* on the common Flax under various conditions. One set was raised in a suitable bed out of doors, the seeds of host and parasite being sown together. The Flax-seeds germinated first, and the young plants were growing vigorously when attacked by the seedlings of the *Cuscuta.* From the same lots of seeds I sowed still more simultaneously in pots of moist earth in a dry and rather cool greenhouse. After the seedlings of Flax and Dodder were well started, I brought half the pots into the laboratory, setting them on a window-sill. The other half I left in the greenhouse. The air of the laboratory, though somewhat warmer than that of the greenhouse, was

much dryer, and of course the illumination which these plants received came mainly from the side. Those plants which remained in the greenhouse throve fairly well, both hosts and parasites, but not so well as those which had been sown at the same time and in similar soil out of doors, while those in the laboratory were plainly unhealthy. Since the hosts did not flourish, the parasites necessarily suffered with them. There were in these three sets of plants three colours: those growing out of doors on healthy, thriving Flax-plants were not only large and strong in appearance, but they were also of the typical pale orange colour; those in the greenhouse were, like their hosts, smaller in size and evidently weaker, and their colour was pale yellow tinged with green; those in the laboratory were the smallest and weakest, and had a decided green colour.

If one cuts off the tips (say eight centimetres long) of healthy branches of a *Cuscuta* and puts them with their cut ends, some in water, and others in a decoction of the usual host (for convenience I used *C. glomerata* and *C. europaea* and their hosts, *Impatiens* and *Chrysanthemum*), cutting off under the surface of the two liquids about one centimetre from the end of each in order to ensure as perfect conduction of the liquids into the branches as possible, one will notice that within eighteen hours the colour has changed, becoming less deep orange; within forty-eight hours they have a plainly green hue; and still later both sets of cuttings will have become nearly as intensely green as the leaves of their usual foster-plants. Those cuttings kept in glasses of water merely, grow somewhat in length, little if any in thickness, but cease within three days to grow at all. Those in the decoction take on the green colour not quite so rapidly, though within a few hours of the others, grow somewhat in thickness, considerably in length, but they too presently cease to grow, and become as deep green as the others. Finally all die. From the water, which was from the general supply of the city (Leipzig), and even from the decoction, only small quantities of organic substances could be absorbed by the cuttings, and in self-

defence they were forced to provide some means of elaborating organic substance for themselves.

It is interesting to note also in this connexion that when plants of *Cuscuta* have, either in nature or in cultivation, fastened upon innutritious or deleterious hosts, they become green in colour just as the cuttings above described. Let branches of *C. Epilinum,* still attached to the mother-plant until they have developed numerous haustoria in the new host, be brought into contact with the stems of some *Euphorbia* of much the same diameter as the stems of Flax. When the haustoria have developed well, say in five or more days after the contact was made, sever the branches from the parent stem. Even before the branches are cut off one can see a change of colour, the orange being paler and perhaps tinged with green ; but soon after they have been cut off they become quite green, and remain so as long as the parasite lives. The Dodder does not, however, flourish on a *Euphorbia,* and after growing weakly for a time, becoming thinner and thinner, it finally dies, and this generally before it has been able to bloom. That the green colour is not altogether, or indeed largely, due to severing the branches from their parent stem, is shown by the fact that branches still attached, which have struck their haustoria into plants of *Euphorbia*, are always weaker than those which have attacked other plants, and also differ from them in colour. That the former do not take on the same deep shade of green as those which are prevented by abscission from drawing any food from the parent is only what we should expect, knowing to how great distances and how abundantly the food secured by more fortunate and well-nourished parts is sent to others less well off. If, instead of letting a branch of Dodder wind about a *Euphorbia*, a *Linum* be used as the new host, abscission of the branch from its parent after the haustoria have well penetrated, causes absolutely no change in colour, for the new host supplies food suitable in quality and quantity. The point of the experiment with *Euphorbia* as host lies not all in the abscission of the branches, but in the development of chlorophyll because

the cuttings do not receive suitable or sufficient food from the plant which they have attacked. That this is really the case is shown also by a continuation of the previously described experiment of putting cuttings of *C. glomerata* on suitable branches of an *Impatiens*. The cuttings become green while they are coiling around and sending haustoria into the host. The green colour remains intense for a few days, then it begins to fade, the new parts are all yellowish, and finally the new plant, with the exception sometimes of the first close coils made, is as yellow or orange in hue as the plant from which it was cut. In this case the lack of suitable food is only temporary, and when it has ceased to exist, the *Cuscuta* no longer needs to be as nearly self-dependent as possible, no longer forms chlorophyll, but returns to its absolutely or almost absolutely parasitic condition. Such, however, is not the case when the branches of *C. Epilinum* are put upon a *Euphorbia*. Although haustoria are formed in numbers adequate to draw from the host food sufficient in quantity, yet the quality of the food, whether owing to the poisonous matters which *Euphorbia* is well known to contain, or owing to less evident causes, is unsuited to the parasite. It never returns to the healthy yellow or orange hue which marks it as a parasitic plant.

When the entrance of haustoria into a stem about which a *Cuscuta* has formed close coils is delayed by thick opposing cuticle, strong sclerenchyma, or intense silicification of the peripheral cells of the host, there takes place in the branch a more or less evident change in colour according as the haustoria attain their goal more or less slowly. Such is the case when branches of *Cuscuta* are brought into contact with leaves of *Aloë*, and with the stems of *Juncus* and *Equisetum*. As might be expected, the parasite does not flourish on these plants, for the difficulty of penetrating them is not set off by more abundant or more nourishing food than that more easily obtainable from other plants. On the contrary, the secretions of the *Aloë* seem to be decidedly poisonous, the haustoria not developing well after they have finally reached the fleshy

interior of the leaves. In *Juncus* and *Equisetum* the haustoria so rarely succeed in uniting with the vascular bundles that from these plants but a small amount of food can be obtained.

The fact that, when occasion demands, the *Cuscuta* can develop a very considerable quantity of chlorophyll which, in the appearance of the plastids which contain it, in their position in the tissues, and in their abundance, justifies the belief that it is a highly functional element of the plant, is most interesting confirmation of the hypothesis that this genus of plants has become parasitic within comparatively recent times and after having attained a fairly complex development such as the other and non-parasitic members of the Convolvulaceae possess. I have as yet had no opportunity of pursuing the interesting questions thus presented, but I hope to be able to do so later.

3. *General relations of Cuscuta to its environment.*

There remain to be discussed one or two general questions concerning the relations of *Cuscuta* to its environment, in view of the conditions necessary for the formation and development of haustoria, before I pass to a consideration of how the haustoria enter the tissues of the host, and attach themselves to the vascular bundles.

As already pointed out, the roots of *Cuscuta* are very feebly geotropic organs. The stems, on the other hand, are strongly negatively geotropic ; for though they may be ready to make close turns about a support, provided the necessary conditions be complied with, yet if rough and thereby irritant rods of suitable size be held horizontally against them no twining will take place. The negative geotropism of the stems is stronger than their irritability. It is to be noticed, however, that when close twining has taken place around a vertical support, and haustoria have been induced by this means, changing the support to a horizontal position does not prevent the haustoria from forming, or delay them in their development. Geotro-

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pism prevents the formation of haustoria only in so far as it prevents the formation of the close spirals, on whose concave surfaces they are normally formed. The biological advantages to the plant in this arrangement are plain and important. Unless it is able to reach the top, or the periphery in general, of its more or less spreading host, its neither large nor conspicuously coloured flowers will fail to attract the attention of those insects by whose visits they are cross-fertilized. Yet if, after having coiled about and having been stimulated to form haustoria against a nutritious support, the accidental bringing of this support to a horizontal position were to stop the formation and development of haustoria, much would be lost and nothing gained. For, by developing the haustoria already induced, the parasite can secure the food obtainable from an otherwise valueless host, and thus the sooner be in condition to seek a better support.

It might be supposed that, if the effect of geotropism were neutralized by revolving both host and parasite horizontally by means of a clinostat, contact would then be sufficient to induce winding about a support placed in any direction. In order to determine whether such is the case or not, I put at different times on the clinostats of Pfeffer and of Wortmann healthy plants of *C. Epilinum*, *C. europaea*, and *C. glomerata*, growing respectively on *Linum*, *Chrysanthemum*, and *Impatiens* (*Sultani* and *parviflora*), which had been growing in pots in the greenhouse long enough to have become thoroughly acclimated, revolving them around a horizontal axis for periods varying from one to five days. In no case did twining take place, however carefully the contacts were maintained. The parasites grew in length in perfectly normal fashion. The absence of irritability to contact was the most noticeable difference from their usual state. Furthermore, a plant taken off the clinostat after having been revolved horizontally and continuously for two or three days around its long axis, was not at once sensitive to contact-irritation. The period of insensibility varies in proportion to the length of time the plant has been upon the clinostat. A plant of *C. europaea*

which had been on the clinostat for seventy-two hours did not begin to form close spirals around a support until twenty-four hours after it had been restored to the vertical position ; then, however, it twined and developed haustoria in the usual time.

If parasite and host be laid horizontally, the parasite will bend upwards as quickly and as sharply as the host, although at the time it may be in contact with a horizontal rod.

As shown so clearly by Wortmann[1], geotropism is such an important factor in the climbing-power of plants that we should not greatly wonder that *Cuscuta* did not wind about horizontal rods either when it was itself erect or horizontal ; for, from the fact that it is only at times that the parasite winds about its support in a way different from that of an unirritable climbing-plant, in other words is irritable only at times, we see how important and how constant the effect of geotropism on its growth must be. But it is surprising that the neutraliza-tion of geotropism by revolving the plant horizontally round its long axis should at the same time obliterate its sensitive-ness to contact. The effect of horizontal revolution on these plants is like the effect of an anæsthetic on animals. Sensi-tiveness is in both cases destroyed temporarily ; in both cases growth can take place as usual throughout the period of insensibility ; and after the removal of the cause of the insen-sibility time must elapse before the organism completely regains all its usual powers.

Though the sensitiveness to contact is destroyed when the effect of geotropism is neutralized by revolving parasite and host horizontally, yet the sensitiveness to light becomes then clearly apparent. Either the heliotropism already existing is merely made evident when the effect of geotropism is removed, or the removal of geotropism as a factor affecting the behaviour of the plant causes it to be more sensitive to light. However this may be, by controlling the direction of illumination one can cause the tips of the parasite, as it is being revolved horizontally with its host on the clinostat, to bend in any

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[1] Wortmann, J., Theorie des Windens, Botanische Zeitung, 1886.

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direction desired.   The stem is positively heliotropic.   Exposure to light from one direction for only six hours will cause the tips to point almost straight toward the source of light. If, however, the plant be simply laid horizontal, and then be illuminated from the side only, that is, so that the effect of heliotropism would be to cause the plant to grow in the horizontal plane, it will be noticed that the tips point almost vertically upwards, plainly showing how much stronger the effect of geotropism is than that of heliotropism, so much stronger indeed that most authors have hitherto agreed in saying that *Cuscuta* is not heliotropic at all.   That it is somewhat heliotropic is proved by the marked effect of light on it when geotropism is excluded.

Light has little effect on the formation of haustoria, and none on the close twining of the plant which usually precedes their formation.   If a branch of *C. glomerata* in contact with a wooden rod be enclosed in a dark chamber, the branch will continue to twine as rapidly and for as long a time as usual, and the formation of haustoria will be begun within the usual length of time after firm contact has been established.   If anything, the branch will twine rather faster in the dark than in the light, and its haustoria will also become evident somewhat earlier ; for this plant is no exception to the general rule that growth is faster at night (that is, in darkness) than during the day.   Plainly the absence of light is no hindrance to the formation of haustoria ; but is light a hindrance ?   They arise within the concave half of the close spiral formed about a host, and this is the darker half, since more light necessarily falls on the outer and convex surface of the coils.   If we cause the formation of haustoria between two leaves held together face to face by two plates of glass, as already described on p. 69, we can determine the effect of light on haustorial formation by illuminating the two sides equally and unequally.   When the two leaves are equally illuminated, the numbers of haustoria on the two sides of the *Cuscuta* are approximately equal.   When one side of the stem receives more light than the other, the haustoria are somewhat

more numerous on the less brightly-lighted side. That there would be a great difference we ought not to expect, for the difference in the illumination of the inner and outer sides of a close-coiled spiral is also not great.

We thus see that, despite the general opinion to the contrary, *Cuscuta* is sensitive to light to a slight extent. Whether it is more sensitive to light (that is, more heliotropic) when it is green I cannot say ; nor would a positive answer to this question be of great value in any way, for it is quite evident from what I have said that the green colour is formed only when the *Cuscuta* is under unfavourable conditions of nourishment. It is well known that other plants almost or entirely devoid of chlorophyll are sensitive to light and are positively heliotropic, and hence it can by no means be inferred that the comparative insensibility of this plant is due to its lack of chlorophyll. It is evident that great sensitiveness to light might frequently interfere with and counterbalance the effect of contact-irritation, and so render the plant unable to secure the necessary food. We must associate this comparative insensibility to light with its mode of attacking and spreading itself over a host, not with the absence of chlorophyll, which is merely a result of the plant's securing an abundance of already elaborated food. The lack of chlorophyll is a degeneration in consequence of parasitism (as seen in many other parasites) ; the neutrality of the plant to light is one of the minor aids to its accomplishing the necessary close windings about a host.

That these plants, especially seedlings, are strongly influenced by moisture I have already pointed out; but that their stems are positively hydrotropic I have been quite unable to see. If they were strongly hydrotropic they would in this way at times defeat their own ends ; for it is possible to conceive that contact-irritation and hydrotropic attraction, working on two sides of the plant and drawing it in opposite directions, might neutralize each other. But hydrotropism, if at all affecting the plant as a positive force, does so only to a slight degree. When geotropism is still exercising its strong

effect, which, far from being opposed to contact-irritation, is in most instances supplementary to it, heliotropism and hydrotropism play a very small part in the economy of these parasites. The two forces which affect the plant most strongly when it is in normal condition are geotropism, which is such an important factor in all climbing plants [1], and contact-irritation, upon which all tendril-bearing plants depend to a greater or less extent for the accomplishment of the purpose for which the tendrils were designed.

Since *Cuscuta* is an annual herb, it, like other such plants, passes through the purely vegetative stage with considerable rapidity. Plants of *Cuscuta* which are cultivated for experimental purposes in a greenhouse attain their maximum of vegetative development somewhat earlier than when cultivated out of doors; but all the species (about ten in number) which have come under my notice, whether growing in a greenhouse or out of doors, were in full flower by the end of July. Up to a certain stage in the growth of a plant, all the buds which form in the axils of the scale-like bracts, the only traces of leaves which these parasites produce, develop into branches which in turn bear only vegetative buds. Presently some of the buds develop into flower-clusters. From this time on more and more buds develop into flowers, until finally few if any give rise to branches. Most of my plants of *C. glomerata* ceased to form new vegetative branches before the end of July, all their energy being devoted to flowering and setting seed. The plants of *C. europaea*, on the other hand, did form a few branches (very few in proportion to the size of the plants) until mid-October, but during the time of maximum flowering it too formed no new vegetative branches. I suspect that the greater hardiness of *Chrysanthemum* as compared with *Impatiens* has a not inconsiderable effect on its parasite, enabling it to vegetate longer than that on *Impatiens*.

The flowers of the three species discussed in this paper are sessile and in dense clusters. Manifestly when the plant is in full flower, there being no new vegetative branches, it is no

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[1] Wortmann, J., Theorie des Windens, Botanische Zeitung, 1886.

longer irritable. The formation of haustoria, which depends upon irritability, which is itself dependent upon growth, is a process that takes place only during the period of active vegetation, or, in the case of *C. europaea,* after the period of maximum blooming is past and a second period of less active vegetation begins. From the time that active vegetative growth ceases and reproductive growth begins, all experimental study of the phenomena of the former must of necessity cease. I attempted by cutting off some of the young branches which were still being formed at the beginning of August on the plants in the Botanic Garden, and setting these as before described upon their appropriate hosts, to secure plants which would for a time at least continue to vegetate. All such efforts were futile. As soon as the cuttings had sent a sufficient number of haustoria (generally two sets were enough) into the hosts to secure an abundance of food, the buds already formed, and whatever new ones had in the meantime been formed, developed into flowers. Similar cuttings made in mid-October and set on Chrysanthemums growing in the greenhouse did not develop more than a few vegetative branches, though having an abundance of flowers.

Chlorophyll may be plainly recognized in certain regions of the plants, at the reproductive stage, mainly in and about the flowers, as others have before stated; but it is not abundant enough more than feebly to supplement the nutrition secured from the host.

In the majority of the plants which I have observed, the largest and finest flower-clusters were situated in or very near regions on which haustoria abounded, that is, on the close spirals. The fewer clusters on the intermediate regions were markedly smaller in themselves, and the flowers which composed them did not attain the size common in others. The advantages of being near the immediate sources of food-supply are so evident that it is unnecessary to enumerate, them: but there is a mechanical advantage also in the comparatively heavy flower-clusters and the still heavier clusters of fruits being borne on the close rather than on the loose,

steep spirals ; for the number of turns within a short distance and the considerably larger diameter of the stem, as well as its being firmly attached to the host by the haustoria, ensure a degree of stability and permanence unattainable in other parts. After the haustoria formed on the close spirals have penetrated, that part of the stem loosely twined in a steep spiral around the host which intervenes between two adjacent groups of haustoria, acts merely as a conductor of food from one part to another. It is no longer of mechanical advantage to the plant, and it therefore soon ceases to grow. Indeed, so slight and so unimportant does the physiological work of conduction eventually become, when no flowers are borne on the intermediate portions of the stem, that they sometimes atrophy and entirely disappear, leaving isolated the short, close spirals bearing clusters of flowers. It is plain, therefore, that the alternating regions of sensitiveness and insensitiveness which are so important in their almost totally distinct ways during the period of active vegetation, continue to be distinct in habits and in importance in the reproductive stage. The unirritable parts were of use in distributing the parasite over as much of its host as possible, and often also in reaching new hosts from which food might at the same time be drawn: the irritable parts fixed the parasite at many points in the wide area won by the rapidly-growing insensitive parts, and at these points developed the haustoria. As repeatedly proved by the experiment of simply severing or of entirely removing the stem between two such regions of haustorial formation, after the haustoria have well penetrated into the host, its further use, even at such early stages in the plant's history, is comparatively trifling. That even in nature the removal of these intermediate segments sometimes takes place, shows how independent of each other the haustorial segments are. One can, by dividing a plant in each of these intermediate regions, produce a number of individuals whose yield of seeds will be as good in quality and quantity as that of undivided plants, provided of course all other conditions are equal. Indeed, it is also possible during the latter part of

the vegetative and throughout the reproductive stage to divide the larger groups of haustoria, which sometimes bear more than one cluster of flowers, without doing any apparent damage. This too sometimes takes place in nature. In Plate VIII, Fig. 1 is shown a petiole of *Solanum jasminoides*, Paxt., around which a *Cuscuta* has twined with many close coils. Only under the four clusters of flowers is any part of the stem to be seen; the rest, above, below, and even in this close haustoria-bearing spiral, has atrophied and finally disappeared, leaving but slight traces. Manifestly these little clusters, each supplied with food by the very small number of haustoria beneath it, have now become individual plants. They remind us of the large and apparently isolated flowers of *Brugmansia* and *Rafflesia*, but we know[1] that the great flowers of *Brugmansia* (and it is the same in *Rafflesia*) are connected with one another by strands of thin-walled merismatic cells running through the cambium of their host. There is nothing, however, either on the surface or in the tissues of the host, which connects these flower-clusters of *Cuscuta*; they are absolutely isolated finally, though of course perfectly and evidently connected at an earlier stage. It is in part owing to its ability to bear, without serious if any injury, division into many small parts, and to its even itself so dividing at times, that the Dodder is such a difficult parasite to exterminate when once it has entered a field.

In most instances the anatomical effects of this parasite on its hosts are not marked. It generally robs them so rapidly and so completely that they sooner or later succumb without having combated its attacks by the formation of any new structures, and even without having shown any renewed growth as a consequence of the intruder's presence. In the petiole figured in Plate VIII, Fig. 1, however, we see a general enlargement of the whole structure and decided

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[1] See Graf zu Solms-Laubach, Die Entwickelung der Blüthe bei *Brugmansia Zippelii*, Botanische Zeitung, 1876; also Die Rafflesiaceae, Engler und Prantl's Die natürlichen Pflanzenfamilien, Lieferung, 35, 1889. G. J. Peirce, loc. cit., p. 318 et seq.

enlargements in the zones where haustoria are most abundant. A section of the petiole at a point about midway between two of the flower-clusters which it bears, that is, at the line *a–b* in Fig. 1, shows (Fig. 2) that, under the single-layered epidermis (*e*) and the two or three layers of collenchyma, come many layers of cortical parenchyma-cells (*c*). Around three sides of the petiole this cortical parenchyma abuts upon the proportionally narrow phloëm-portion (*b*) of the vascular tissues. The phloëm consists mainly of sieve-tubes and bast-parenchyma, only small and scattered groups of bast-fibres being found. Separated from the phloëm by a single-layered cambium is the broad xylem (*x*), composed of rather small ducts and, in much larger proportion, of thick-walled wood-fibres. At one side, bordering upon the phloëm, is the small bundle (*l*) which runs to one of the leaflets. The vascular ring of the petiole, enclosing the pith (*p*) in which are a mass of sclerenchyma-cells (*s'*) and small scattered groups of scle-renchyma-fibres in the region marked (*s*), is incomplete on the upper side of the petiole, and here the cortical merges directly into the pith-parenchyma. An aborted haustorium is shown at *H*. The haustorium aborted probably because of the absence in this region of vascular tissues with which it could unite. After its abortion, and after the atrophy and fall of the parasitic stem which gave rise to it, this atrophy being hastened, though, I think, scarcely caused by the abortion of the haustorium, it became covered over by the epidermis of the petiole. Such aborted and partly or entirely covered haustoria are the only remaining traces of the former presence of a continuous stem wound around the petiole, and these are few in number.

If one now compares this section with the one shown in Plate VIII, Fig. 3, which is at the line *c–d* in Fig. 1, one sees at once that the larger size of the petiole at this point is due to the increase in the number of layers of parenchyma-cells in the cortex (*c*), to the formation in it of two sets (*s'*, *s'*) of sclerenchyma-masses, to the greater width of the band of wood (*x*), in which the proportion of fibres to ducts is even greater

than before, and to the presence of the large haustorium (*H*) whose phloëm- and xylem-elements have united with those of the petiole. On the upper side, the region *p*, which in the section represented in Fig. 2 was composed of ordinary spheroidal parenchyma-cells, has been the seat of considerable changes. The cells composing it have been compressed laterally into elongated forms, their long axes being at right angles to the surface, by the bending round of the incomplete vascular ring which was divided and forced apart by the intruding haustorial wedge (*H*). These cells, elongated by pressure, were then divided by cross-walls at right angles with their long axes and parallel to the direction of the compressing force. Finally a considerable thickening and lignification of the walls of all of these cells, and of some adjacent cells which had not been so much compressed and had not divided, took place. Thus, by forming between the two ends of the incomplete vascular ring a compact mass of not easily compressed cells, the petiole can resist, though still with little effect, the intrusion and growth of the haustorium. In the region *s*, as shown in Fig. 2, sclerenchyma-fibres are formed in small groups; but in the section represented in Fig. 3 they are decidedly more numerous. The walls of these cells too are thicker and more strongly lignified. In other respects the characters and proportions of the component tissues of the petiole remain unaffected by the presence of the active haustorium.

We have seen that peripheral tissues difficult of penetration (such as those of *Aloë, Juncus, Equisetum*); that vascular bundles so scattered and so surrounded by resistant elements (as in *Juncus* and *Equisetum*) that the union of the haustoria with them is difficult and infrequent; that tissues containing poisonous matters (as in *Aloë* and *Euphorbia*), are great protections for a plant against the attacks of *Cuscuta*. Anatomical changes taking place after the haustoria have penetrated avail little, as the petiole of *Solanum* illustrates. But many plants resist attacks successfully merely because they are too large to be embraced by the parasite.

Unlike the Fungi, which find easier entrance and more suitable conditions for growth and development when a plant is ailing, *Cuscuta* flourishes the better in proportion as the hosts are stronger, healthier, more able to supply it abundantly with food without being forced soon to succumb to the constant drain. It is a distinct disadvantage to the Dodder when its host dies before it has itself come into flower and set seed. Its cycle of development is not so simple that it can rapidly be run through; it demands much food and strong mechanical support in order that its flowers may be advantageously displayed for the visits of insects, and that its fruits may successfully disseminate the seeds which they contain. Weak hosts cannot nourish well; hosts which easily succumb after being attacked do not afford the necessary mechanical support; and hosts which vegetate for only a short season, dying away either to the root or entirely, cannot assist in seed-dissemination.

II. THE PENETRATION OF THE HAUSTORIA INTO THE HOST.

1. *Penetration due to Mechanical Force.*

The various conditions affecting the origin and the development of the haustoria of three species of *Cuscuta* have been discussed in the foregoing pages. There remain to be considered in this paper the means by which the haustoria already formed in the parent plant make their way into the host and attach their xylem- and phloëm-elements to the corresponding elements of its vascular bundles. In my previous paper on certain phanerogamic parasites [1] my treatment of this part of the subject was regrettably incomplete, because, at the time of writing, only alcohol-material was at my disposal. From the living plants which it has since been my good fortune to be able to observe and to experiment upon, I am able to add to what I then wrote.

Manifestly in one or both of two ways only can the parasite

[1] Loc. cit.

ordinarily secure the penetration of its haustoria into a host; by mechanical pressure, or by chemical action, or by a combination of both. In my previous paper I expressed the opinion, based on the appearance of the excellent alcohol-material which I had examined, that the haustoria made their way by solution. I still believe this to be true, and I shall presently give some experimental evidence in favour of this view. I said nothing about pressure, for the evidences of pressure were very slight. The following experiments demonstrating that both solution and pressure accompany the intrusion of the haustoria into the host will show how necessary it was to supplement purely histological examination by physiological experiment. The plants used in the experiments now to be described were either *C. glomerata* or *C. europaea*, the plants of *C. Epilinum* by the time these experiments were begun having almost ceased to vegetate, developing only flowers and fruits.

If a branch of *C. glomerata* of suitable age be brought into contact with such a plant as *Zea Mais* at a part small enough in diameter to allow the branch to make close coils about it, haustoria will be produced. The branch should not be placed against the stem, which is protected by a peripheral ring of hard sclerenchyma, but rather against the base of a leaf still wrapped around the young stem, the whole diameter of stem and enclosing leaf being not more than one centimetre. After the haustoria first formed have penetrated the leaf, the leaf and the attached parasite should be cut away. Selecting, by the aid of a hand-lens, a haustorium which has developed to the point of entering the leaf but has not yet done so, careful transverse sections of the leaf should be made at this point, passing through and including the parasite which is attached to, though it has not yet penetrated into, the host. (The method of attachment is discussed in division II. 2 of this paper.) Taking for examination the section through the centre of the haustorium, the structure of the leaf will be seen to be as follows (see Pl. VIII, Fig. 4). The upper surface (the lower, *c–d*, in the figure), which so near the

base is of course the inner one and is more or less closely applied to the stem, consists of rather small thin-walled epidermal cells whose continuity is rarely broken by stomata. Immediately underlying this layer are the usual spongy parenchyma-cells which make up the larger part of the thickness of the leaf. At fairly regular intervals groups of these cells, about ten in each group, immediately underlying the epidermis, become more thick-walled and elongated, forming slender strands running lengthwise in the leaf, and thus adding something to its strength. The parenchyma-cells in the centre are large, thin-walled, spheroidal, and are adjoined by parenchyma-cells of similar character except that they are smaller in proportion as they are nearer the surfaces of the leaf. The under part of the leaf, the outer owing to its vertical position in embracing the stem, contains the large vascular bundles, whose course is longitudinal. These bundles project into the mesophyll, are separated from one another by considerable masses of parenchyma, and are surrounded individually by strongly lignified sheaths. The endodermis of each bundle is continuous with a plano-convex mass of sclerenchyma-cells which abuts by its plane side upon the epidermis. The epidermis of the lower side of the leaf consists of smaller cells with thicker walls, and is more frequently broken by stomata, than the epidermis of the other side. Except directly opposite the vascular bundles, where it adjoins the masses of sclerenchyma-cells, this lower epidermis, like the other, is in contact with the mesophyll-parenchyma.

Turning now to the parasite, we notice that the papillate cells of the epidermal cushion, which overlies the developing haustorium, have become so firmly applied to the epidermis of the leaf that their tips are flattened. The diameter of the whole cushion is about twice as long as the distance between two vascular bundles in the leaf. The young haustorium, developing in the cortical matrix of its parent, will be variously influenced by the resistance offered to the pressure which by its growth it exerts, and it will naturally, other

things being equal, grow in the direction of least resistance. Manifestly there will be less resistance to its forward growth midway between two vascular bundles of the Maize-leaf than directly opposite one of them ; and against this intermediate region it pushes the epidermal and cortical cells which overlie it. It has been many times observed that even against strongly resisting rods of wood and glass the haustoria cause swellings of the stem by their growth. In the case now under discussion such a swelling directly over the tip of the haustorium is being pushed by the continued growth of the haustorium against the epidermal and parenchymatous tissues of the leaf which are situated between two vascular bundles (see Fig. 4). The epidermis of the leaf is pushed in by the low, blunt, conical swelling on the parasite, causing collapse of the larger, thinner-walled parenchyma-cells which are just behind it.

Passing to a somewhat older haustorium on the same coil, and sectioning it and the leaf to which it is attached, one sees that the continued and increasing pressure finally results in the rupture of the epidermal cells of the leaf. The epidermis is an elastic, tough, strongly-resisting layer. When it is broken through, the further progress of the haustorium by means of mechanical pressure is comparatively easy until it meets the thick-walled and strongly lignified cells of the endodermis of the bundles. In every experiment which I performed with *Zea* the haustoria failed to unite with the bundles ; and hence the branches, which had been severed from the parent plants after the haustoria had penetrated the leaves, presently died.

Of course in the above case the pressure brought to bear upon the leaf was exercised by the haustorium only indirectly ; it grew in size and length, and thereby pushed the adjacent cortical cells away from it ; these in turn pushed forward the epidermal cells ; these epidermal cells were rejuvenated by the contact and stimulated by the nutritious host to grow into papillae of very considerable size. In this cumulative manner a swelling arose on the surface of the parasite. By the con-

tinuation of these processes the swelling constantly increased in size, but more especially in height, and pressed the epidermal cells which had already been for some time in contact with the host more and more strongly against it. From their nature and arrangement the peripheral tissues of this host could not resist or transfer the pressure; they were forced to bend in and collapse ; and so the pressure became evident. A moment's study of the much more delicate and yielding stem of *Impatiens Balsamina* will show how its peripheral tissues are affected by the pressure of the growing haustorium. Immediately underlying the single-layered epidermis which covers this essentially cylindrical stem, are five layers of collenchyma-cells which form a fairly strong and decidedly elastic ring about the deeper tissues. Within this ring are five or six layers of large rather thin-walled parenchyma-cells which in turn enclose the more or less continuous ring of vascular bundles. There is an abundant central pith. We see that the stem is composed of four concentric rings enclosing a core of pith. These rings are not rigid, for they are composed, except the wood, of elastic and not thick-walled cells with larger or smaller air-spaces between them. Even the wood is composed of comparatively thin-walled ducts and fibres, and is so frequently traversed by medullary rays that this ring also is anything but rigid. Hence pressure exerted upon one part of the stem can be transferred to and divided among all parts, a slight change of form of the whole stem allowing the cells in the region first pressed upon to escape for a considerable time much if not all injury from this cause. Furthermore, the structure of the stem is such that horizontal pressure is not only distributed among the cells on the same plane, but among those above and below also, and so its effects are rendered still less evident. If it were not that the host is tightly embraced within the close spiral formed by the parasite, we could conceive of its being able, by sufficient change of form, to escape being penetrated by the haustorium which, after all, is able to exert only a limited amount of pressure; but no stem strong enough to be

erect is able to do this, especially when it is enclosed by the
parasite wound tightly and many times about it, for it is not
yielding enough.

That the pressure exercised by the growing haustorium of
C. glomerata is very considerable, though so completely
masked by the yielding nature of the stems and petioles of
the species of *Impatiens* upon which it is parasitic, may be
readily demonstrated thus. Wind a sheet of tin-foil four or
five centimetres long and only wide enough to meet, not to
overlap, around a stem or erect branch of *Impatiens* of suitable
size, fastening it by binding bast. Bring into contact with the
stem thus enwrapped a healthy branch of the parasite. Close
coils will be formed and haustoria will also be induced by the
contact. Their formation and growth cause the usual swel-
lings, and these press with constantly augmenting force
against the tin-foil. Finally the foil is ruptured, tearing in
irregular fashion, and thus allows (see Fig. 5) the epidermal
cells covering the irregular protruding mass to come into
contact with the host. The haustorium continues to grow
and presently makes its way into the host. If the tin-foil be
wound twice about the host, the haustoria fail to penetrate
the foil, though making marked impressions in it ; and they
become abortive just as when they are formed in consequence
of contact with other innutritious supports such as glass or
wood. The tin-foil used in this experiment was two-tenths
of a millimetre in thickness and of good quality. Through it
the host could exercise no chemical influence on the parasite,
nor could the parasite excrete a solvent of the metal. Hence
we see that very considerable pressure is exerted by the
growing haustorium and the epidermal cells immediately
overlying it, and that pressure alone is sufficient to accomplish
penetration into the host.

Such pressure is paralleled by that exercised by normal
roots, whether they be lateral or main ones. Prunet[1] has
again called attention to this in a paper on the penetra-

[1] Prunet, M. A., Sur la perforation des tubercules de Pomme de Terre par les
rhizomes des Chiendents, Revue Générale de Botanique, III, 1891.

E

tion of potato-tubers by the rhizomes of 'Quitch Grass' (*Agropyrum repens*, Beauv.). From experiments of my own on seedlings of various plants producing both large and small main roots, it is perfectly evident that the power of penetrating living tissues by pressure alone is not a peculiarity of haustoria (which are but lateral roots modified in origin and structure to accomplish a very special purpose), nor of the roots of some Grasses. If a root be so firmly fixed against a plant that, if it grows at all, it can only grow into the opposing tissues, it will invariably penetrate them. Into how solid tissues these ordinary roots can make their way it is not within the scope of this paper to discuss. It is sufficient now to state that they readily penetrate through tissues as solid as the cortical tissues of any of the hosts of *Cuscuta* which I have yet seen. As recently determined by Pfeffer[1], the pressures which ordinary roots are able to exert are great. Accurate determinations of the pressures exerted by haustoria are, on account of the habits of the plants, most difficult to make ; but from the celerity and apparent ease with which the haustoria of *C. glomerata* penetrate tin-foil it is hard to suppose that they are the weakest of all roots.

From the foregoing experiment it becomes evident that, though one object of the close coils formed about its host is to produce intimate contact of a considerable area of the parasite with its host, in order to induce the formation of numerous haustoria, there is still another and also a very important object. Owing to the closeness of the coils and to the large area consequently applied to the host, any force acting between the parasite and the host and tending to push them apart, would be resisted by the very great friction which must be overcome before the parasite could be made to uncoil. This resistance is not far from the breaking-strength of the stem. The force developed by the growing haustoria tends to push host and parasite apart, and it is resisted in this way. But the matter is not so simple. After a branch has made

[1] Pfeffer, W., Druck- und Arbeitsleistung durch wachsende Pflanzen. Abhandl. d. K. S. Gesellschaft d. Wissenschaften, XXXIII, 1893.

a close, nearly horizontal turn about the host, the curved part still continues for a time to grow in length. It is true that this growth is neither rapid nor of long duration, yet it is sufficient to loosen the spiral somewhat, to weaken the contact, to reduce the stimulus for haustorial formation, to lessen . the force which the growing haustoria can bring to bear on the host, by increasing the distance through which they must grow. However, accompanying and following this comparatively slight growth in length is a very considerable and long-continued growth in thickness. The result of this latter is more than to counterbalance the growth in length. It maintains the closeness of the spiral, it constantly increases the intimacy of the contact, it strengthens thereby the stimulus for haustorial formation, and supplements the force which the growing haustoria can bring to bear on the host, by reducing the distance through which they must grow. This growth in thickness further supplements the force by (first) causing the stem of the parasite to press against and thus to compress the host by its whole concave side, and not merely by the swellings over the young haustoria ; and (second) by increasing the rigidity of the coils so that, firmly braced by the coiled stem in which their strong bases are embedded, the haustoria can apply all their force forwards and against the host. Besides, the parasite is not merely closely pressed and firmly held against the host, but, as I shall demonstrate, is actually attached to it by many of the epidermal cells covering the swellings over the haustoria.

That the stem of the parasite, whether it bear haustoria or not, and whether it be coiled closely or only steeply and loosely around the host, exercises a very considerable pressure, might be suspected from its resemblance to tendrils and twining stems, but it may be made quite evident by the simple method used in demonstrating, though not thereby measuring, the pressure of tendrils, and the relative pressures developed by the two sorts of coils will at the same time be indicated. Let a branch of *Cuscuta* which is irritable, and therefore in condition to make close turns, be brought into

E 2

contact with a glass rod whose average diameter is known; and another branch, which is not in the irritable stage, be brought into such a relation with another rod of the same diameter that it will make steep turns about it. After both branches have twined about the supports for from thirty-six to forty-eight hours, remove the rods with as little disturbance of the coils as possible. It will at once be noticed that the diameter of both coils decreases, and that the number of turns increases proportionally. After waiting from twelve to twenty-four hours, the contraction will have reached its maximum and have become permanent. By measuring now the average diameters of the two imaginary cylinders enclosed by the gradual and the steep spirals respectively, by the close turns formed in consequence of irritation and by the loose turns formed without irritation (that is, as a climbing plant would form them), we find that the diameter of the former is from one-half to three-quarters the diameter of the rod first employed, whereas the diameter of the latter is never less than three-quarters the diameter of the rod. Evidently the steep spiral, formed only for supporting the plant as it ascends, exercises little if any more than enough pressure on the support to keep the plant from slipping down by its own weight; whilst the close spiral, formed in consequence of irritation for the purpose of forming an intimate and enduring contact and for enabling the haustoria the more readily to penetrate the host, exercises very considerable pressure. As shown before, the pressure exercised by the closely coiled stem is still more increased by the formation and growth of the haustoria.

But the force brought to bear on the host by the parasite, whether through the gradual or the steep spirals, is not merely one of compression; for by its circumnutation the parasite exercises a force which, unfortunately, has not yet been determined. We must therefore recognize two sorts of force which are applied to the host; a deflective, exercised by circumnutation, and a compressive, exercised by the coils and the haustoria growing in and from them. Doubtless the sum

of these two, when it is possible to estimate them in mechanical units, will be found surprisingly large when the delicacy of the plant developing them is taken into consideration.

2. *Penetration by the chemical activity of the pre-haustorium.*

Von Mohl [1] noticed that when a *Cuscuta* had wound about a polished silver rod, the positions of the haustoria against this rod were indicated, after the plant had been untwined from the support, by spots of a glairy fluid or of a shiny dry deposit. This he believed to be a mucilaginous matter which the parasite exuded in order the better to fasten itself to the host. L. Koch [2] considers it to be a solvent which is secreted for the purpose of softening if not dissolving the opposing tissues of the host, but he gives no experimental proof of this hypothesis. There are in the host three sorts of matter which may be affected by the parasite: the cell-walls, composed of cellulose and more or less infiltrated matter; the starch and other carbohydrates in solid form; and the nitrogenous substances. Though the haustorium may be able by mechanical pressure alone to penetrate the tissues and to bring its vascular elements into direct contact with the phloëm and xylem of the host, yet it goes without saying that it would be greatly to the advantage of the parasite were it able to supplement physical force by chemical action, and thus not only to make penetration easier, but also to allow the cells of the haustorium to dissolve, and thus to bring into available form, the solid nutritive matters around them. I have demonstrated in the foregoing pages that both contact and nourishment are necessary to the full development of haustoria. I shall now describe certain experiments showing some of the ways in which this nourishment is obtained.

Let a mixture of two parts plaster of Paris and one part of starch (I used the large-grained starches of potato and barley), very thoroughly stirred together, be wetted with

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[1] Mohl, H. v., loc. cit. (cited by Koch on p. 55).
[2] Koch, L., loc. cit., 1880, pp. 56, 57.

a small quantity of water and cast into rods of about six centimetres length and less than one centimetre diameter. These may be sterilized just before using by soaking for fifteen minutes in ether and then rapidly evaporating under diminished atmospheric pressure. Into a moist chamber made of large glass-tubing, such as I have previously described (page 75), which has been thoroughly sterilized, insert the irritable tip of a branch of *C. glomerata*, and by sterilized forceps place the rod of plaster and starch in the chamber and in contact with the branch, quickly closing the chamber. In the course of six days the branch should have twined and developed several haustoria. Cutting the branch from its parent, remove it, still in contact with the rod, from the chamber. By a clean flat-pointed needle remove some of the starch and plaster from directly under a haustorium and examine it in water under a microscope. With another clean flat needle remove some of the starch and plaster from some part of the periphery of the rod far removed from any haustoria, and examine it also in water. It will be noticed that on the first slide, of material from under a haustorium, the proportion of starch to plaster is smaller than in the original mixture, and that most of the starch-grains still to be found are corroded in various degrees (see Pl. VIII, Fig. 6). The corrosion proceeds in the majority from the centre of the grain toward the periphery, forming broad and more or less radial canals; but a very considerable number of grains show the corrosion beginning at the periphery and running in, or beginning at several points between periphery and centre. In the last case, the corrosion proceeds from several centres instead of from one, but finally a common cavity is made by their union in the centre of the grain. Examination of the second slide, of material far from the influence of haustoria, will show that the proportion of starch to plaster is approximately the same as that of the original mixture[1], and that none of the starch-grains are corroded.

[1] It is scarcely to be expected that the ingredients should have been so perfectly mixed that their proportions would not vary somewhat in different parts of the rod.

If now the tip of a haustorial swelling be cut off and examined with a little of the starch and plaster still adhering, it will be seen that the haustorium has not penetrated the overlying epidermis, but that the epidermal cells have become papillate, and that most of the starch-grains still existing, either in contact with or very near the papillae, are deeply corroded. The corroded starch-grains can more accurately be observed, however, if after cutting off a bit of the stem in contact with the rod, some of the mixture still adhering to the tips of the haustorial swellings be removed to a slide, spread out thereon, and examined in a drop of water.

Evidently then the starch in contact with and in the vicinity of the papillate epidermal cells has been acted upon by them. That starch-grains not in contact with these cells are also acted upon shows that the ferment which is secreted is capable of diffusion for some distance through plaster of Paris, however limited may be its power of diffusion through colloids[1]. Examination of the plaster and starch with which unmodified epidermal cells are in contact, that is, between the haustorial swellings, shows no corrosion ; the starch-grains are as unacted upon as those from parts of the rod far from the *Cuscuta*. The papillate cells are as well developed as those formed when the parasite is in contact with a host, showing that they have been nourished by what they have dissolved. The haustoria, though not so far advanced as they would be in the same length of time had a living plant been used instead of a rod, have yet developed farther than they would had an entirely insoluble and innutritious support like glass been used. The solvent action of the papillate cells results, therefore, in the acquisition of food used not only by themselves but by the haustoria also.

Since starch is contained within the cortical tissues of the host, it remains to be shown whether the papillate epidermal cells of the parasite reach this food-supply merely by rupturing

[1] Brown, H. T., and Morris, G. H., A Contribution to the Chemistry and Physiology of Foliage Leaves. Journ. Chem. Society, London, May, 1893, pp. 656-8.

the cells in which it is stored, or whether by a less violent
process they are enabled to act upon it. One can demonstrate
this by means of a slender stick of elder-pith impregnated
with a nutrient solution, as was used in determining the condi-
tions for haustorial formation (see p. 76). Let such a stick
of pith be put in contact with the irritable part of a branch of
Cuscuta enclosed in a moist chamber of large glass-tubing,
quickly closing the chamber. After a few days, the *Cuscuta*
having made many turns about the stick and bearing haustoria
in several stages of development, one may sever the branch
from the parent and remove it, still in contact with the pith,
from the chamber. Sections through haustorial swellings
which seem firmly fixed in some way to the pith, will demon-
strate that the papillate epidermal cells are as large and
healthy as normal, and that some of them have penetrated
the cells of the pith to a greater or less depth, some even into
the third row from the surface. These pith-cells seem little
compressed, certainly not collapsed or ruptured. Clearing
thin sections by means of equal parts of glycerine and water,
and examining them under a high power of the microscope,
we see that the epidermal cells have entered the cavities of
the pith-cells through holes in the walls. These holes corre-
spond with considerable accuracy to the shape and size of the
cell or cells passing through them (Fig. 7). By staining with
chlor-iodide of zinc and washing away the excess by distilled
water before clearing in the mixture of glycerine and water,
the result will be made still more evident ; for the difference
in composition of the cell-walls of the pith and of the *Cuscuta*,
with the resulting differences in the shades of blue produced
by the reagent, and the presence of protoplasm and nucleus
(stained yellow or brown) in the cells of the parasite and the
absence of these structures in the pith-cells, enables one to see
very clearly that not by pressure alone could the epidermal
cells have thus made their entrance. These epidermal cells,
collectively forming the ' pre-haustorium,' must have secreted
an enzyme which at least has softened and, since one can see
no broken pieces of cell-wall turned back or pushed to one

side by the intruders, undoubtedly also dissolved the cellulose. By this solvent action exerted on the walls of the cortical cells of the host, the food-substances contained therein can be reached and be appropriated later by the papillate cells. The holes thus dissolved, constantly increasing in number and, as I shall presently show, in size by the solvent action of the cells at the tip of the haustorium proper, enable the young haustorium to grow rapidly forward through but feebly opposing tissues toward the conducting-tissues of its host. That the cellulose thus dissolved is probably consumed by the parasite is indicated by the normal, development of the papillate epidermal cells, and the very considerable develop-ment of the haustoria formed by those branches twined about sticks of pith saturated with decoctions. For, though the decoction is nutritious at first, it so rapidly deteriorates in nutritive value that it can be useful for only a short time, and the pith, containing of itself no food of any kind except the cellulose of its walls, must be extremely innutritious.

The epidermis which covers a haustorial swelling consists of two sorts of modified cells: those lying directly over the haustorium become separate from one another, except at their bases, and grow out into long papillae: those surrounding them, and therefore not in, though parallel with, the line which the growing haustorium will follow in penetrating the host, elongate but do not separate from one another, and hence do not become papillate. The walls at their tips are very nearly as thin as those of the papillae. Both sorts of cells come into intimate contact with the walls of the epidermal cells of the host. The papillate cells exercise a solvent action so ener-getic that holes are made through the walls of those cells that oppose their further growth. The non-papillate cells, like the others in the kind, but not in the amount, of new growth which they accomplish, also excrete a solvent through their terminal walls, but the quantity of solvent excreted is not large. By this means only a partial solution of the walls of the epidermal cells of the host with which they are in contact takes place, but the walls of the contiguous cells of parasite and host

become fused together so perfectly that (Fig. 4) they are quite indistinguishable from one another. This union is very firm, as is shown by the resistance encountered in tearing the parasite away from its host even before the haustoria have penetrated. This union is sometimes broken after a time by the pushing apart of parasite and host owing to the forcible penetration of the haustorium through not readily soluble tissues, but in such cases the walls of the cells, once firmly united and then torn apart, are irregular and ragged.

I have already pointed out (p. 61) that the parasite can twine about leaves and send haustoria into them. The curve of the parasite about the lamina of a leaf can be only an ellipse. Manifestly in such a case as this there can be but little of the mechanical advantage which aids the haustoria in penetrating an approximately cylindrical stem. The stem of the parasite no longer furnishes an unyielding brace on which the haustoria are based; consequently it will be pushed away from the surface of the leaf by the growth of the haustorial swellings, just as the leaf too bends away under the same pressure. Evidently by pressure alone the haustoria would only with great difficulty penetrate the leaf. The rejuvenated epidermal cells of the parasite, however, perform the same work as before. The tips of the non-papillate ' cushion-cells ' fuse with the walls (which they partially dissolve) of the opposite epidermal cells of the leaf, and the leaf is thus securely held. The papillate cells, collectively the 'pre-haustorium,' perforate the walls of the cells opposite them by a more complete solution than that accomplished by the ' cushion-cells,' and, growing through the holes thus made, enter the mesophyll. Held fast against the leaf by the ' cushion-cells,' and anchored by the pre-haustorial papillae, the stem of the parasite can now brace, and so assist, the haustoria in their forward growth. Although one ' cushion-cell ' holds parasite and host but feebly together, yet there are so many of them that the attachment becomes very firm. The area of attachment is large ; through the centre of this area the haustorium grows; its tip is conical, not blunt, and

hence meets with less resistance ; its way has been partly excavated by the papillate cells. Hence the haustorium, growing along a partly made way in the line of least resistance, usually brings to bear on the attaching cells no more strain than they are able to bear.

We see in the results of the experiments just described additional reason for distinguishing in the 'cushion' of older authors which overlies the young and growing haustorium, two sorts of epidermal cells. The long papillate cells in the centre dissolve a passage for the permanent and much more effective haustorium proper; they use and transfer to other parts the nutritive substances which, after having dissolved them, they can readily absorb. Their functions are certainly those of a haustorium, and therefore I have ventured to call them collectively the 'pre-haustorium.' The other modified epidermal cells may justly retain the name of 'cushion-cells,' though, as I have just shown, their function is plainly that of hold-fasts.

We see, therefore, that Von Mohl's observation previously cited, that these cells pour out a secretion, was a correct one ; but his opinion that the secreted substance is a mucilaginous matter was a mistaken one, though the object, that of cementing the two plants together, is attained by the partial solution accomplished by small quantities of the enzyme and the subsequent fusion of the two adjacent walls.

3. *Penetration by the chemical activity of the haustorium.*

Experimental demonstration that the haustorium itself exerts chemical, as well as mechanical, action on the cells which oppose its growth, is difficult, owing to the relatively innutritious supports composed of lifeless organic matter which are the only ones that may be used. For, though it seems improbable, yet it might be possible that living cells, irritated by the contact or the nearness of the intruding organ, would be stimulated into secreting a solvent by which their own walls would be broken down. Yet if such were really the

case we should expect to find not merely small parts of the wall, and these of shape and size proportioned to the attacking cells, but large portions gone, in fact a general disorganization of the tissue in the region attacked. No such changes in the attacked tissues of a host occur, and hence we cannot suppose that the host destroys its own tissues to any extent. That the haustorial cells are chemically active is strongly indicated in two ways. First, a study merely of alcohol-material inclines the observer to doubt that such accurate adjustment of the phloëm- and xylem-elements in the central cylinder of the growing haustorium with the phloëm- and xylem-elements of a vascular bundle of the host could be accomplished by mechanical means alone. How accurate this adjustment is, even to the correspondence of thick and thin areas in the walls of the haustorial tracheids with similar areas in the walls of the tracheae of the host to which they apply them-selves, I have already demonstrated[1]. Second, thin sections of young haustoria of *C. glomerata* in the fleshy stems or petioles of *Impatiens Balsamina* show that the long papillate cells at the tips of the haustoria pass through the walls of the opposing parenchyma-cells of the host in the same way as do the papillate cells of the pre-haustorium.

In the experiment with elder-pith it is evident that the dead pith-cells cannot form new walls, but in a living plant one must determine accurately whether, when a papillate haustorial cell applies itself to a living parenchyma-cell of the host, the wall of the parenchyma-cell be simply pressed in by the force of the growing haustorial cell ; whether the natural extensibility of the cell-wall thus being gradually pushed into the cavity of the cell, be supplemented by growth leading to the development of the at first shallow depression into a cup, and finally a cylindrical pocket, enclosing the haustorial cell ; or whether there is actual perforation of the wall of the paren-chyma-cell, and whether the thin wall of the papilla is in actual contact with the protoplasmic and other contents of the cell into which it has grown. A careful study of thin and

[1] Loc. cit. p. 300.

well-cleared sections of a young haustorium in the thick cor-
tical parenchyma of a fairly large, fleshy stem, of *Impatiens*
will show that the course of events is as follows[1]. A papillate
cell at the tip of the haustorium becomes, by its growth in
length, closely applied to the wall of a parenchyma-cell. By
the pressure produced by more growth the tip is flattened
against the opposing wall and becomes slightly enlarged.
Presently the wall of the parenchyma-cell becomes gradually
thinner and more incurved within the circular line described
by the flattened tip of the pressing haustorial cell (see
Pl. VIII, Fig. 8). When the haustorial papilla first comes
into contact with the wall of the opposing parenchyma-cell,
one can plainly distinguish the two walls from one another
without the aid of staining agents; but by using a solu-
tion of the chlor-iodide of zinc the walls of the two cells
become differentially stained. The wall of the cortical paren-
chyma-cell may be thicker than that of the haustorial cell,
and may for this reason be more intensely stained; but
besides this difference in quantity of colour, one sees also
a difference in quality, for the cellulose of the younger papil-
late-cell becomes red purple, rather than blue purple, as the
other does. When, however, the tip of the haustorial cell has
been for a time pressed and thereby flattened against the wall
of the parenchyma-cell, and the wall of the latter has begun
both to bend and to grow thinner at the point of contact, the
most careful staining and examination under a high magnify-
ing power fail to reveal any line separating the two. The
two walls, by the partial solution of that of the parenchyma-
cell at least, and, I think, of that of the papilla also, have
become fused into one (Fig. 8). Finally, by the combined
action of solution and pressure, the tip of the papillate haus-
torial cell enters the cavity of the parenchyma-cell, pushing
the protoplasm and nucleus to one side in some cases (Fig. 9),
or more commonly penetrating, but otherwise not disturbing
the protoplasm in any way. Furthermore, as Fig. 10 shows,
the haustorial papilla becomes fused, at the region where it

[1] Compare pp. 307, 308 and figures 16ᵃ, 16ᵇ, and 16ᶜ in my former paper.

passes (at generally a right angle) through the wall of the parenchyma-cell, with the wall of that cell, so that not only does no opening by the side of the papilla exist, but it is impossible to determine exactly where the wall of the parenchyma-cell ends.   The fusion is so perfect that the transition from older to newer cellulose, from parenchyma-wall to papilla-wall, is most gradual; they have modified each other in their perfect union.   It seems to me by no means improbable, though micro-chemical and optical proofs are still wanting, that the rapid growth of the haustorial papillae is in part at least made possible by the walls which cover their tips not being quite solid; that indeed the enzyme which dissolves the walls of opposing cells also keeps the walls at the tips of the cells which secrete it in partial solution, and therefore in such condition that they but slightly resist the forward pressure from within.   Careful staining by chlor-iodide of zinc, or by various agents producing more enduring stains (e. g. Congo Red), fails to show the slightest evidence that the wall of the cortical parenchyma-cell persists as a sheath around the papilla, and that the protoplasmic and other substances in its cavity are separated and protected from the haustorial cell by an involution of its wall.   Its wall has become a constituent and indistinguishable part of the wall of the intruding cell, acting no longer as a protection against, but as a part of, the intruder.

We thus see that the haustorial cells penetrate those opposed to them.   That this penetration is accomplished by means of chemical action as well as by pressure we see from the walls with which they come into contact becoming thinner at the points of contact as they bend in, and finally disappearing at these points, and from the fact that the holes through which the intruding cells pass are accurately proportioned to them in form and size.   Through the repeated perforation of their walls by successive haustorial cells, the cortical cells which oppose the progress of the haustorium are removed, and along this tunnelled way the young haustorium reaches, and finally applies itself to, the conducting tissues of

the host. The starch-grains in the cells thus attacked and penetrated disappear, being dissolved and consumed by the protoplasm of the cells which contain them, or by the intruders; by which, it is of course impossible to tell.

We have seen that the penetration of the host by the parasite is begun by the pre-haustorium overlying the young haustorium proper, and that this is accomplished by the combined action of pressure and solution. The time and the field of action of the pre-haustorium are manifestly limited owing to its position, for the growing haustorium must finally crush and push through it. Some arrangement must be made to continue the work of the pre-haustorium, and this is effected by the cells at the tip of the haustorium, cells corresponding in position to those of the cap of a typical root. They become in appearance as in function like those composing the pre-haustorium, long, slender, thin-walled, with abundant protoplasmic contents and large nuclei, and great capacity for growth.

SUMMARY.

The results of the experiments described in the preceding pages may be briefly summarized as follows. The genus *Cuscuta* comprises parasitic climbing plants with two distinct modes of twining. At certain stages they resemble the majority of twining climbers in that they twine steeply, and only tightly enough to secure necessary mechanical support. They do not twine about horizontal rods whether they themselves be erect or horizontal. They twine in the direction in which they nutate; so far as I have been able to see, always in the reverse direction of the hands of a watch. At other stages, which regularly alternate with the foregoing, they make short, close, much more nearly horizontal turns about a vertical support, thereby embracing it closely and bringing their concave surfaces into intimate contact therewith. The former turns are made solely in consequence of the climbing habits of the plant, by the combined effects of circumnutation

and geotropism.   The latter are induced by contact-irritation, which causes a modification of the manner and an acceleration in the speed of coiling.

Haustoria are ordinarily formed only upon the concave surfaces of the close coils.   They also are the result of irrita-tion, their formation being induced by contact of sufficient duration.   Their development depends upon both contact and nourishment ; without the one or the other only partial development takes place.   The formation and perfect develop-ment of haustoria may take place on one as well as on another side of the stem, or on opposite sides at one and the same time, it being equally irritable on all sides, provided only the necessary contact and nourishment be supplied.   They appear almost exclusively on the concave side of the close curves only, because there the contact-irritation is greatest ; they develop best there because both contact and nourishment are on that side.   Each haustorium is formed as a result of contact with an irritant object over the place of its origin. Innocuous liquids and wet gelatine are not irritant objects.

The periodic irritability of *Cuscuta* can be temporarily destroyed by revolving the plant horizontally around its long axis; that is, by neutralizing the effects of geotropism.   In ordinary conditions geotropism is stronger than irritability, for the plant will not twine about horizontal supports ; though, when a once vertical support about which a branch has closely twined is laid horizontally, the formation and development of haustoria already induced go on unhindered.   In ordinary conditions these plants are not markedly heliotropic or hydro-tropic ; but when the effects of geotropism are neutralized by horizontal revolution on the clinostat, the plants become more sensitive to light and moisture.   The comparative insensitive-ness to light is not due to the absence of chlorophyll, nor is chlorophyll always absent.   It is formed whenever for any reason the plant is insufficiently nourished, and the amount formed (that is, the intensity of the green colour) may be used as an index of the amount of organic food which it is receiving.

These parasites can attack successfully only those plants

whose size, peripheral tissues, internal structure, cell-contents and secretions, allow their being closely embraced by the parasites, their being readily penetrated by the haustoria, the speedy union of the conducting-tissues of the haustoria with their conducting tissues, while no poisonous effects are produced by cell-contents or secretions. The effects on the host are mainly physiological, it rarely happening that anatomical changes take place in consequence of the presence of haustoria.

Finally, the haustoria penetrate by means of mechanical pressure, of the chemical activity of the pre-haustoria, of the chemical activity of the cells at the tips of the haustoria proper; and these processes are aided, and in part shared in, by the cushion-cells.

I wish to express my warmest appreciation of and heartiest thanks for the numberless kindnesses which Professor Pfeffer and his assistants have constantly shown me in my work. Without their suggestions and criticisms but a small part of the investigation just described could have been accomplished.

F

EXPLANATION OF FIGURES IN PLATE VIII.

Illustrating Mr. Peirce's paper on *Cuscuta*.   (Tissues of parasite red.)

Fig. 1. Part of petiole of *Solanum jasminoides* on which are scattered flower-clusters of a *Cuscuta*, the intermediate portions of the stem having atrophied and disappeared.   Natural size.

Fig. 2. Outline of cross-section of petiole in Fig. 1, through line *a–b*, between two flower-clusters. *e*, epidermis; *c*, cortical parenchyma; *b*, phloëm; *x*, xylem; *s'*, sclerenchyma-mass; *s*, area in which are scattered sclerenchyma-masses; *p*, pith-parenchyma; *l*, bundle to leaflet; *H*, imbedded abortive haustorium. × 12.

Fig. 3. Outline of cross-section of petiole in Fig. 1, through line *c–d*, through a flower-cluster and one of its haustoria, *e*, *c*, &c., as above; except *p*, where parenchyma-cells have divided, become thicker-walled and lignified, under pressure. × 12.

Fig. 4. Cross-section of leaf of *Zea Mais* (*b*) showing pressure exerted by growing haustorium of *C. glomerata* (*a*); *c–d*, epidermis of upper (inner) side of leaf. × 120.

Fig. 5. Showing penetration by pressure of the growing haustorium of overlying cells through sheet of tin-foil: *a–b*, sheet of foil in cross-section : *C. glomerata*. × 120.

Fig. 6. Starch-grains of *Hordeum* corroded by cells of pre-haustorium of *C. glomerata*.   × 490.

Fig. 7. Cross-section of elder-pith showing solution of its cell-walls by 'cushion-cells' of *C. europaea*.   × 490.

Fig. 8.   Cortical parenchyma of petiole of *Impatiens Balsamina*, in which wall of haustorial cell of *C. glomerata* has partly dissolved, bent, and is fused with wall of cortical parenchyma-cell.   × 360.

Fig. 9. Showing penetration into cavity of parenchyma-cell by solution accomplished by haustorial cell, whose wall at *a* and *b* has fused with wall of parenchyma-cell.   × 360.

VITA.

I, GEORGE JAMES PEIRCE, Protestant in religion, was born in Manilla, in the Philippine Islands, on the 13th of March, 1868. My parents were Americans, temporarily resident in that Spanish possession. My father, George Henry Peirce, a commission merchant, was born in Portland, Maine; my mother, Lydia Ellen Peirce, whose maiden name was Eaton, was born in Boston, Massachusetts. My parents remained in Manilla until I was nearly six years old. Then, my father being out of health from overwork in that taxing tropical climate, they started to return to America, taking me with them, going by way of Singapore and the Suez Canal. My father died on the way, in Cairo, Egypt. My mother pursued her journey viâ France and England, and reached home in April 1874. After spending three winters in Columbia, South Carolina, the summers being passed in New England, my mother settled in Cambridge, Massachusetts. Then I attended the public schools of the city until, in 1886, I was admitted to the Lawrence Scientific School of Harvard University. I pursued the so-called Biological Course, in which I devoted myself more to Botany than to Zoology, and in 1890 received the degree of Bachelor of Science. I was then appointed Assistant in Botany, and held the position for two years. In 1892 the Corporation of Harvard University awarded me one of the Parker Fellowships, and in 1893 renewed the award. I have by this means been able to study in Europe. I spent the Winter Semester 1892–3 under Professor Strasburger in Bonn, and have since then been under Professor Pfeffer's instruction at this University.

To my honoured teachers, especially to those who have trained me in scientific directions, Professors Goodale, Farlow, Mark, Shaler, Jackson, Hill in America; and Professors Strasburger, Pfeffer, Leuckart, Wiedemann, Fischer, Ambronn in Germany, I wish to express my most hearty thanks and devotion.